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VOLUME 54

1985

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TAXONOMIC STATUS OF DORMICE (GENUS *GRAPHIURUS*) FROM WEST AND CENTRAL AFRICA

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Abstract

Additional records of occurrence, measurements, and life history data are given for five species of dormice, genus *Graphiurus,* from northwestern Zaire and Cameroon. For the first time *Graphiurus olga* (Thomas, 1925) is reported from Cameroon and *G. christyi* Dollman, 1914, from northwestern Zaire. Nomenclatural relationships of the nominal taxa of small species of *Graphiurus,* including *G. coupeii* (Cuvier, 1822), *G. orobinus* (Wagner, 1845), and *G. kelleni* (Reuvens, 1890), are discussed.

Introduction

The species of *Graphiurus* occurring in southern Cameroon were reviewed by Robbins and Schlitter (1981). Their interpretation of the systematic status of the species of dormice in this region differed from that expressed by Genest-Villard (1979) in her revision of the genus. Studies of recent additions to the collections of dormice (genus *Graphiurus*) contribute to our knowledge of the geographic distribution and taxonomic relationships of the species occurring in the northwestern Zaire and Cameroon.

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Submitted 29 May 1984.

MATERIALS AND METHODS

Cranial measurements, based on those listed by Robbins and Schlitter (1981), were taken to the nearest 0.1 mm with dial calipers. Length of hind foot includes claws; height of rostrum was taken behind incisors. All specimens are deposited in the collection of mammals at Carnegie Museum of Natural History (CM), unless indicated otherwise. Also, specimens were examined in the collection of the British Museum (Natural History), London (BMNH); The Museum, Texas Tech University, Lubbock (TTU); and the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM).

ACCOUNTS OF SPECIES

Graphiurus christyi Dollman, 1914

Graphiurus christyi Dollman, Revue Zool. Africain, 4:80, 25 July 1914.

Type locality.—Mambaka and Mambo, Belgian Congo [=Zaire].

Specimens examined (8).—ZAIRE: Bumba Zone, Yalosemba (7 CM, 1 TTU).

Measurements.—See Table 1.

Remarks.—*Graphiurus christyi* was reported from Lolodorf, Cameroon (Robbins and Schlitter, 1981:282). The nearest localities in Zaire are from Buta (Schouteden, 1946:464) and Gambi, southeast of Angu (Robbins and Schlitter, 1981:282). The specimens from Yalosemba reported here help bridge the hiatus in the geographic distribution in this species (Fig. 1).

The eight specimens from Yalosemba in northwestern Zaire are measurably larger than those from eastern Zaire and Cameroon reported (Table 1) by Robbins and Schlitter (1981:274–276). However, the characteristic shape of the skull, especially the projecting nasal and premaxillae region, and the color of the pelage of the Yalosemba specimens are identical to specimens of this species from northeastern Zaire.

All of the specimens from Zaire show the dark brownish staining of the forelegs and chest described by Hatt (1940:474) for a number of species of dormice from throughout the range of the genus.

Graphiurus crassicaudatus (Jentink, 1888)

Claviglis crassicaudatus Jentink, Notes Leyden Mus., 10:41, April 1888.

Type locality.—Oban District, southwestern Nigeria.

Specimens examined (1).—CAMEROON: 4 km S, 2 km E Eseka (1 CM).

Remarks.—Although seldom encountered, *Graphiurus crassicaudatus* occurs throughout the forested region of Cameroon. A single adult male was captured by hand on 15 August 1978. The individual was living in a hole in a concrete culvert under a railroad. This and other similar holes resulted from trapped air next to the wooden frames when the concrete culvert was poured *in situ.* A small stream flowed

Table 1. —*Selected cranial measurements of two species of* Graphiurus. *Measurements of the respective holotypes from the British Museum (Natural History) are listed.*

Specimens	Measurements												
	Greatest length of skull	Condylo-basal length	Zygo-matic breadth	Inter-orbital breadth	Breadth of brain-case	Greatest length of nasals	Length of anterior palatine foramina	Length of maxillary toothrow	Greatest breadth across second upper molars	Length of bulla	Breadth of bulla	Length of palate	Height of rostrum
					Graphiurus christyi								
CM 86748 ♂	29.7	26.6	16.0	4.7	12.6	11.0	3.2	3.4	5.9	7.7	5.8	11.1	5.7
CM 86749 ♂	29.8	26.7	16.6	4.8	13.1	11.0	3.2	3.2	6.2	7.7	6.1	11.2	5.9
CM 86750 ♂	29.8	26.7	15.7	4.9	12.8	11.1	3.4	3.2	5.9	8.0	5.7	11.4	5.7
CM 86751 ♂	29.1	—	16.2	5.0	13.1	10.8	3.1	3.3	6.3	7.8	5.9	—	5.6
CM 86753 ♂	29.8	26.6	16.0	4.8	13.1	11.2	3.1	3.1	5.9	7.9	5.9	10.9	5.5
BM(NH) 14.2.11.8 ♂	—	—	15.2	4.6	12.2	10.1	2.5	3.2	—	7.0	5.3	10.3	5.3
					Graphiurus olga								
CM 59454 ♂	21.6	19.1	11.9	3.8	10.8	7.6	2.7	2.5	4.4	6.1	4.6	8.1	3.7
BM(NH) 25.55.12.32 ♀	23.0	20.7	12.6	3.8	—	8.2	2.8	2.6	4.9	6.5	5.2	8.3	3.9

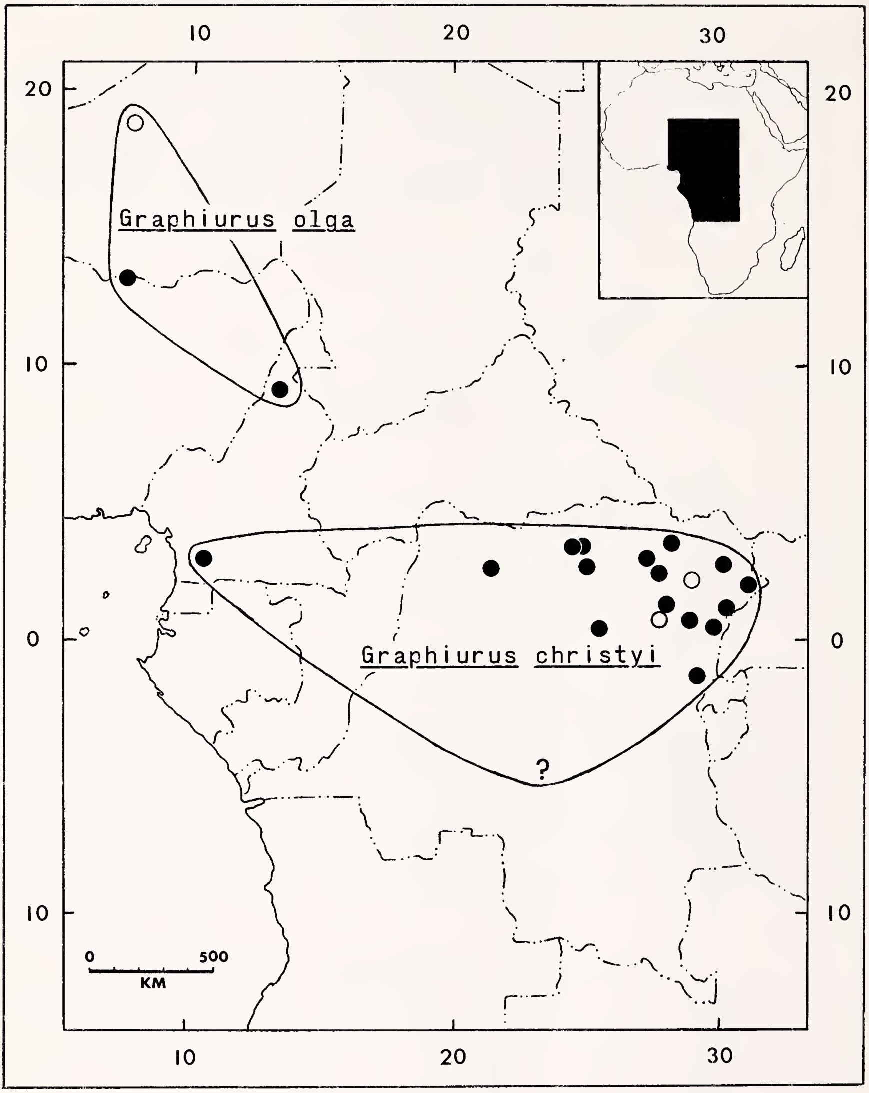

Fig. 1.—Map of Equatorial West Africa and adjacent region showing distributions of *Graphiurus christyi* and *G. olga*. Open circles represent type localities; type locality for *G. christyi* involves co-localities. Locality for Ikongo, Zaire, is queried as it represents a literature record of doubtful identity. Literature records for *G. olga* from Niger and Nigeria are from Thomas, 1925. Those for *G. christyi* are as follows: Cameroon, Robbins and Schlitter, 1981, and Zaire, Dollman, 1914; Thomas, 1915; Wettstein-Westersheim, 1923; Hatt, 1940; and Schouteden, 1946.

through the culvert. The animal had testes measuring 16 by 7 mm and it weighed 29 g. Another individual was sighted but escaped capture.

No specimens of this species of dormouse were collected in northwestern Zaire.

Graphiurus hueti (Rochebrune, 1883)

Aethoglis hueti Rochebrune, Actes Soc. Linn. de Bordeaux, (4) 7:110, 1883.

Type locality.—Environs of St. Louis, Sorres, Senegal.

Specimens examined (4).—CAMEROON: 13 km S, 8 km E Ambam (1 CM); 18 km S, 9 km E Ambam (2 CM); 22 km S, 1 km E Ambam (1 CM).

Remarks.—Four specimens of *Graphiurus hueti* were taken from hollow trees while collecting the tree-roosting bats *Nycteris grandis* and *Hipposideros cyclops.* Two adult females, weighing 100 g and 87 g, were not pregnant when collected on 30 July and 1 August 1978. Two adult males collected on 31 July 1978 weighed 110 and 115 g and had testes measuring 20 and 21 mm, respectively.

Although local hunters examined numerous hollow trees at the localities in northwestern Zaire, no individuals of *Graphiurus hueti* were encountered. Neither Schouteden (1946) nor Misonne (1974) report this species from Zaire.

Graphiurus lorraineus Dollman, 1910

Graphiurus lorraineus Dollman, Ann. Mag. Nat. Hist., (8) 5:184, March 1910.

Type locality.—Molegue, south of Setema Rapids, Welle River, Belgian Congo [=Zaire].

Specimens examined (14).—CAMEROON: 11 km S, 1 km E Bamenda, 1900 m (5 CM). ZAIRE: Bumba Zone, Yalosemba (7 CM); Gemena Zone, Tandala (2 CM).

Remarks.—*Graphiurus lorraineus* is widely distributed and frequently common in forested and second growth situations in West and Equatorial Africa. Near Bamenda, five adults were captured in Sherman non-folding live traps set in low trees and undergrowth in a forested ravine. The same habitat harbored numerous individuals of *Aethosciurus cooperi.*

An adult female collected near Bamenda on 24 August 1978 had no embryos. A juvenile male and a subadult female were taken at Yalosemba on 10 and 18 June 1979, respectively. In northeastern Zaire, Hatt (1940:475) reported nestlings in mid-April and half-grown young from early January and mid-November.

Graphiurus olga (Thomas, 1925)

Claviglis olga Thomas, Ann. Mag. Nat. Hist., (9) 16:191, July 1925.

Type locality.—Tehsiderak [=Tassederek], Air, 2350 ft, Niger.

Specimens examined (2).—CAMEROON: 23 km S, 8 km E Garoua (1 CM). NIGER: Tehsiderak (1 BMNH, holotype).

Measurements.—See Table 1.

Remarks.—These are the first records of this small dormouse from Cameroon and this brings the number of species of *Graphiurus* known from Cameroon to six (Robbins and Schlitter, 1981). In the original description, Thomas (1925:191) reported two specimens from Dan Kaba, Nigeria, as well as three individuals from the type locality in Niger. We have not examined any additional specimens of this species. The single adult male was taken on 20 July 1978 in a Sherman folding aluminum live trap, set in a tree in a forested area in a marsh. The type locality of this species is also a seasonal marsh on the western side of the Air Mountains of Niger. Each of the specimens weighed 12 g.

DISCUSSION

The taxonomic relationships of the small dormice in the genus *Graphiurus* have become more confusing in recent years. In the early parts of the twentieth century, it was recognized that a large species (usually referred to as *G. murinus*) and a small species existed in the savannah zones from western Africa skirting the high forest zone to southern Africa. In eastern Africa for example, Hollister (1919:152) separated out the small species and called in *G. parvus.* In Angola, Hill and Carter (1941:78–81) referred to the small species as *G. kelleni,* with greatest skull length listed by them as (Hill and Carter, 1941:186) 23.2 mm, and the large species as *G. ansorgei* rather than *G. murinus.* However, further confusion was introduced by Ellerman (1940:610) who included *Myoxus coupeii* Cuvier, 1822, which was described from Senegal as a synonym of nominate *G. murinus* from the Cape of Good Hope. At the same time, he (Ellerman, 1940:610) separated *Eliomys microtis* Noack, 1887, which was described from the west side of Lake Tanganyika, as a distinct species even though Allen (1939:309) placed Noack's taxon as a junior synonym of *G. murinus.* Considering the number of nominal taxa described from the intervening areas, it seems unlikely that any of these taxa would be junior synonyms of *G. murinus* described from the Cape of Good Hope.

Until a number of the earlier described nominal taxa are identified, confusion will continue with these two groups. There are a number of available names for those small individuals with greatest length of skull between 21 and 25 mm. Genest-Villard (1979:399) considered *G. par-*

vus (True, 1893) as the oldest available name for these small individuals. Other nominal taxa which we believe refer to the small species are as follows: *G. kelleni* (Reuvens, 1890); *G. smithii* (Thomas, 1893); *G. nanus* (De Winton, 1897); *G. johnstoni* (Thomas, 1898); *G. brockmani* Dollman, 1910; *G. parvus dollmani* Osgood, 1910; *G. personatus* Heller, 1911; *G. brockmani internus* Dollman, 1912; and *G. olga* (Thomas, 1925).

However, until two of the oldest names available, namely *Myoxus coupeii* Cuvier, 1822, and *Myoxus orobinus* Wagner, 1845, are properly identified, the available name for this small species must remain in doubt. Although we have not examined the holotype of *G. kelleni* in Leiden, Hill and Carter (1941:186) show in their table of measurements that this is a small species. It would seem that *G. kelleni* is the oldest name of *Graphiurus* available at this time, at least for the southern and eastern African species of smallest dormouse.

Rosevear (1969:509) remarked on the taxonomic status of *G. coupeii* based on his examination of the original description and colored plate. He (1969:610) compared the *G. olga* material in the collections of the British Museum (Natural History) with the description of *G. coupeii.* From this comparison, Rosevear (1969:610) noted two differences—*G. olga* was noticeably smaller, and the description of *G. coupeii* clearly stated that the belly hairs of this taxon were pure white, not white-tipped as in *G. olga.* We believe this description of belly hairs of *G. coupeii* to probably be in error as we have seen no dormice from any part of Africa with totally white belly hairs.

We have examined two specimens from Kudang, Gambia (USNM 377688 and 377689). These two specimens are similar to other West African *G. lorraineus* as understood by Robbins and Schlitter (1981) and not with *G. olga* as understood in this report. If these two Gambian specimens do represent *G. coupeii,* then that name would become the oldest name for the West African *G. lorraineus.* Detailed study of specimens from western West Africa is required in order to properly identify *G. coupeii.* In any case, we believe that *G. olga* is a species distinct from *G. lorraineus* and *G. murinus,* although it may prove to be conspecific with *G. kelleni* and *G. parvus.*

Myoxus orobinus Wagner, 1845, was originally reported from Sennaar, Sudan. Setzer (1956) did not examine any specimens of this species and no additional specimens of dormice seem to have been collected from the Sennaar region. Setzer (1956:544) considered *G. orobinus* to be a species smaller than *G. mirinus* based on Wagner's (1845:149) description. We have examined the original description and are unable to allocate the taxon from the description. The description of color does not distinguish this taxon and the only measurement given is for body length, which is insufficient to separate these two similar-sized species groups. Unless either a holotype is found or other specimens of dormice are collected in the Sennaar region, we believe that this name will prove unidentifiable if based only on its description.

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GAZETTEER

Coordinates are listed for localities for specimens examined, cited literature records, and places mapped in Fig. 1. Abbreviations for countries are as follows: C = Cameroon; G = Gambia; N = Nigeria; NR = Niger; and Z = Zaire.

Ambam (C)	2°23′N, 11°16′E	Lolodorf (C)	3°14′N, 10°48′E
Angu (Z)	3°30′N, 24°27′E	Mambaka (Z)	0°51′N, 27°33′E
Arebi (Z)	2°47′N, 29°35′E	Mambo (Z)	2°12′N, 28°20′E
Avakubi (Z)	1°18′N, 27°35′E	Masisi (Z)	1°25′ S, 28°50′E
Bamenda (C)	5°55′N, 10°12′E	Medje (Z)	2°25′N, 27°18′E
Beni-Cartoushi (Z)	0°44′N, 29°34′E	Niangara (Z)	3°45′N, 27°52′E
Buta (Z)	2°49′N, 24°50′E	Poko (Z)	3°08′N, 26°58′E
Dan Kaba (N)	13°12′N, 7°44′E	Selemani (Z)	0°54′N, 29°52′E
Djugu (Z)	1°55′N, 30°32′E	Stanleyville (Z)	0°33′N, 25°14′E
Eseka (C)	3°39′N, 10°46′E	Tandala (Z)	2°58′N, 19°21′E
Gambi (Z)	3°28′N, 24°31′E	Tehsiderak (NR)	18°52′N, 7°43′E
Garoua (C)	9°20′N, 13°20′E	Ukaika (Z)	0°45′N, 28°45′E
Inkongo (Z)	4°55′ S, 23°15′E	Yalosemba (Z)	2°35′N, 21°47′E
Kudang (G)	13°40′N, 15°04′W		

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FOUR NEW SUBSPECIES OF *AMEIVA AUBERI* (SAURIA, TEIIDAE) FROM THE BAHAMA ISLANDS

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Abstract

Four undescribed subspecies of *Ameiva auberi* Cocteau are named from the Bahama Islands; three of these are from Andros Island and the fourth from Green Cay.

Introduction

Ameiva auberi Cocteau is a species of teiid lizard known from the Bahama Islands, Cuba, and the Isla de la Juventud (=Isla de Pinos). Throughout its range it is the only species of the genus, with no sympatric congeners. In the Bahamas, *A. auberi* is widespread on the Great Bahama Bank, from which eight subspecies are known. McCoy (1970) studied *Ameiva* from most major island groups and islands on the Great Bahama Bank, but only 31 specimens from Andros Island. McCoy (1970) considered that number "inadequate for analysis of intra-island variation." The largest number of these specimens was from Gibson Cay, the type-locality of *A. a. kingi* McCoy. Since 1970, over 200 additional specimens have been collected from Andros Island. It is the purpose of this study to demonstrate the presence there of at least three more subspecies of *A. auberi.* Also included here is an assessment of the status of the *Ameiva* population of Green Cay. It has been previously noted (McCoy, 1970) that the *Ameiva* of this island are more similar

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Table 1.—*Means of scale counts and twice standard errors of means of seven populations of* Ameiva auberi *from the Bahama Islands. Data for* A. a. bilateralis *have been taken and modified from McCoy (1970:149).*

Subspecies	N	GAB	Femoral pores	15th CV	4th toe
vulturnus	21	104.8 ± 1.8	26.2 ± 1.2	28.4 ± .75	75.7 ± 1.8
vulturnus × *kingi*	103	105.1 ± 1.2	26.3 ± 0.4	29.1 ± .31	76.5 ± 0.8
kingi	14	98.0 ± 5.3	25.9 ± 1.6	27.7 ± .51	73.5 ± 2.3
behringensis	18	101.7 ± 2.4	25.9 ± 0.8	28.7 ± .52	75.8 ± 1.4
sideroxylon	69	97.4 ± 1.7	27.9 ± 0.6	29.1 ± .49	76.5 ± 1.2
parvinsulae	17	102.3 ± 2.6	24.1 ± 0.6	29.9 ± .51	72.5 ± 1.5
bilateralis	38	103.6 ± 1.0	24.1 ± 0.3	28.7 ± .21	75.9 ± 0.5

to *A. a. bilateralis* of the Ragged Islands than to the populations of geographically closer islands. We have named the Green Cay population and present basic comparisons with other Bahamian populations of *A. auberi.*

TAXONOMIC ACCOUNT

Ameiva auberi sideroxylon, new subspecies

Holotype.—Carnegie Museum of Natural History (CM) 60539, an adult male, taken 4.8 km N Mastic Point, Andros Island, Bahama Islands, on 30 November 1976, by James A. Rodgers, Jr. Original number Albert Schwartz Field Series (ASFS) V16015.

Paratypes (all from Andros Island, Bahama Islands).—ASFS V16016–29, same data as holotype; ASFS V13751, Mastic Point, 10 March 1958, D. W. Buden; ASFS V16033–56, 1.6 km N Stafford Creek, 1 December 1968, J. A. Rodgers, Jr., A. Schwartz; ASFS V20267–68, 1.6 km N Stafford Creek, 5 September 1970, D. C. Fowler; ASFS V20269–73, Blanket Sound, 5 September 1970, D. C. Fowler.

Associated specimens.—All from Andros Island, as follows: ASFS V16013, 3.2 km SE Red Bay; ASFS V20274–81, 1.6 km N Standiard Creek; ASFS V20265–66, 2.9 km NW Fresh Creek; ASFS 10287–93, ASFS V20317–18, ASFS V23548, ASFS V27971, Fresh Creek; ASFS V20285, 0.8 km S Fresh Creek; ASFS 10.1 km N Fresh Creek; ASFS V20333–38, Owen's Town; ASFS V16057–58, 1.6 km N Owen's Town; ASFS V23800–01, 0.8 km N Owen's Town; NCSMNH (North Carolina State Museum of Natural History) 5097, Morgan's Bluff Road, Ashton's Cave, ca. 1 km SSE Coleby Bay; NCSMNH 353, Atela Coppice, ca. 16.5 km NNW Stafford Creek settlement; NCSMNH 4663–64, 4666, Owen's Town, ca. 6.5 km W Stafford Creek settlement, 2.5 km W London Creek; NCSMNH 5672, across Fresh Creek from Andros Town.

Definition.—A Bahamian subspecies of *Ameiva auberi* occurring on Andros Island, characterized by a combination of small size (males to 87 mm, females to 74 mm snout–vent length), low number of midbody granules (mean = 97.4 ± 1.74), high number of femoral pores (mean = 27.9 ± .59); see Table 1 for details. Dorsal lines persistent in both sexes, varying in color from bright yellow to gray-yellow or cream, dorsal fields brick to reddish brown, lateral fields black with some brick dotting along margins, interlimb line black, usually present, in some individuals extending onto the tail; males with chest, throat, and mesoptychium black; tail gray.

Distribution.—North Andros, from Red Bay in the northwest and Owen's Town in the interior, and along the east coast from the vicinity of Mastic Point south to the vicinity of Fresh Creek (Fig. 1).

Description of holotype.—An adult male with the following measurements and counts: snout–vent length (SVL) 87 mm, tail 187 mm; dorsal granules at mid-body (GAB) 95; femoral pores 13 and 13 (total 26); 28 scales in the 15th caudal verticil; fourth toe subdigital scales 35 and 35 (total 70). Dorsal fields (in life) rich reddish brown (almost bronze), middorsal line dull gray-yellow, dorsolateral lines yellow (not bright). Lateral fields black, with dotted brick edging; top of head suffused with black; lateral line gray. Chin, throat, mesoptychium, chest, and first eight rows of ventrals black, diffusing into blue-gray posterior venter; infralabials blue-gray.

Comparisons.—*Ameiva a. sideroxylon* is small in size compared with the other *Ameiva* populations on Andros Island. In GAB counts, *A. a. sideroxylon* is significantly (equals non-overlap of twice standard errors of means) lower than *A. a. behringensis* and *A. a. vulturnus* (see beyond) but is very close to *A. a. kingi.* In 15th caudal verticil counts *A. a. sideroxylon* is moderately higher than *A. a. behringensis* and *A. a. vulturnus,* and significantly higher than *A. a. kingi.* In femoral pore counts *A. a. sideroxylon* is significantly higher than the other *Ameiva* populations of Andros Island.

The dorsal fields in *A. a. sideroxylon* are brown, darker than in the other Andros populations. The interlimb line (=lateral stripe of McCoy, 1970) is a line below the lateral field extending from the front leg to the rear leg; in *A. a. sideroxylon* this line is black, and in some specimens extends onto the tail. The middorsal stripe is clear anteriorly, outlined by black, but fades posteriorly. This is similar to *A. a. kingi,* but quite different from the pale markings of other Andros populations. Black markings are limited to the chin, chest, and mesoptychium of *A. a. sideroxylon* males, unlike the corresponding markings on other Andros *Ameiva,* in which the color extends farther onto the chest. *Ameiva a. sideroxylon* has the most distinctly brick-red lateral field edging of any of the Andros *Ameiva* populations; on other populations the edges are more tannish.

Etymology.—The name *sideroxylon* is derived from the former generic name of the mastic, *Mastichondendron foetidissimum,* in allusion to the type-locality.

Ameiva auberi behringensis, new subspecies

Holotype.—CM 60540, an adult male, taken at Behring Point, Andros Island, Bahama Islands, on 6 September 1970, by D. C. Fowler. Original number ASFS V20299.

Paratypes (all from Andros Island, Bahama Islands).—ASFS V20300–14, same data as holotype; ASFS V20298, 9.0 km N Behring Point, 6 September 1970, D. C. Fowler; ASFS V20316, 7 km N Behring Point, 6 September 1970, D. C. Fowler; NCSMNH 5672, 2 km N, 1 km W Cargill settlement on main road, 9 April 1981, R. E. Ashton, Jr.

Definition.—A Bahamian subspecies of *A. auberi* occurring on Andros Island, characterized by a combination of moderate size (males to 98 mm, females to 50 mm SVL), moderate number of mid-body granules (mean = 101.7 ± 2.4), moderate number of femoral pores (mean = 25.9 ± .84); dorsal fields tan, median dorsal line nearly invisible in males, more distinct in females. Lateral fields black, with brick to tan edging. Males with throat, chest, and mesoptychium black; venter blue. Females with ventral ground color white, never blue, dorsolateral and ventrolateral lines paler than in males.

Distribution.—Coastal region of central Andros near Behring Point. All specimens were taken within 10 km of Behring Point (Fig. 1).

Description of holotype.—An adult male with the following measurements and counts: SVL 98 mm, tail 280 mm; GAB 103; femoral pores 13 and 13 (total 26); 30 scales in the 15th caudal verticil; fourth toe subdigital scales 37 and 38 (total 75). Dorsal fields (in life) tan; middorsal line very pale, dorsolateral lines faintly yellow, ventrolateral line creamy, lateral fields black with brick to tan edging. Chin, throat, mesoptychium, and first six ventral scale rows black, gradually diffusing into bright blue venter.

Comparisons.—*Ameiva a. behringensis* is moderate in size among Andros *Ameiva* populations. In GAB counts, *A. a. behringensis* is higher than *A. a. kingi,* significantly higher than *A. a. sideroxylon,* but lower than *A. a. vulturnus.* In 15th caudal verticil counts *A. a. behringensis* is higher than *A. a. kingi,* slightly higher than *A. a. vulturnus,* and lower than *A. a. sideroxylon.* In femoral pore counts, *A. a. behringensis* is very close to *A. a. kingi* and *A. a. vulturnus,* but significantly lower than *A. a. sideroxylon.*

The dorsal fields in *A. a. behringensis* are tan, lighter than in *A. a. sideroxylon* or *A. a. kingi,* but darker than in *A. a. vulturnus.* The interlimb line is distinctly gray, better defined than the hazier line of *A. a. kingi,* but not so dark as in *A. a. sideroxylon* and *A. a. vulturnus.* In *A. a. behringensis* males, the middorsal stripe is almost invisible. On females, it is clear anteriorly, fading posteriorly, and outlined in black. This is almost identical to the condition, in both sexes, of *A. a. sideroxylon.* The faintness of this stripe in males is also seen in *A. a. vulturnus,* but in females of the latter subspecies, the stripe is bordered by black at the base of the head, rather than posteriorly. On *A. a. kingi* the line is clearly visible in both sexes. The throat and chest are black; this black area is not so extensive as in *A. a. kingi* and *A. a. vulturnus,* but is more extensive than in *A. a. sideroxylon.* The lateral fields have brick to tan edging, slightly lighter than that of *A. a. sideroxylon* but more conspicuous than in *A. a. kingi* and *A. a. vulturnus.*

Etymology.—The name *behringensis* is derived from the type-locality, Behring Point.

Ameiva auberi vulturnus, new subspecies

Holotype.—CM 60541, an adult male, taken at Marsh Bay, Andros Island, Bahama Islands, on 1 June 1972, by M. T. Felix. Original number ASFS V22348.

Paratypes (all from Andros Island, Bahama Islands).—ASFS V22349–52, same data as holotype; ASFS 22353–56, 5.3 km S Deep Creek, 1 June 1970, A. Schwartz; ASFS V22336–43, Congo Town, 31 May 1970, M. T. Felix; ASFS V22330–33, 1.6 km N Congo Town, 30 May 1970, A. Schwartz.

Definition.—A Bahamian subspecies of *Ameiva auberi* occurring on Andros Island, characterized by a combination of moderate size (males to 94 mm, females to 67 mm SVL), high number of midbody granules ($\bar{x} = 104.8 \pm 1.78$), moderate number of femoral pores ($\bar{x} = 26.2 \pm 1.23$); dorsal lines very pale in males, more distinct in females; dorsal fields sandy tan, lateral fields black with tan edging, dorsolateral and ventrolateral lines cream, broad, and very distinct; interlimb line broad, black-gray; tail tan, gray-tan above; males with throat, mesoptychium, and chest black, with black marks occasionally extending to vent.

Distribution.—South Andros, from Congo Town in the north, along the coast at least to Marsh Bay in the south.

Description of holotype.—An adult male with the following measurements and counts: SVL 94 mm, tail 221 mm; GAB 105; femoral pores 13 and 14 (total 27); 32 scales in the 15th caudal verticil; fourth toe subdigital scales 38 and 38 (total 76); dorsal ground color (in life) sandy tan, ventral ground color in adult males blue; middorsal stripe very faint tan; lateral fields black with tan edges; chin, throat, mesoptychium, and chest to the fourth ventral scale row black, suffusing posteriorly into blue ventral color.

Comparisons.—*Ameiva a. vulturnus* is intermediate in size among the *A. auberi* subspecies of Andros Island. In GAB counts, *A. a. vulturnus* is significantly higher than *A. a. sideroxylon* and *A. a. kingi.* In 15th caudal verticil counts, *A. a. vulturnus* occupies a position of intermediacy, slightly higher than *A. a. kingi,* but lower than *A. a. sideroxylon* and *A. a. behringensis.* In femoral pore counts, *A. a. vulturnus* is almost identical to *A. a. kingi* and *A. a. behringensis* but lower than *A. a. sideroxylon.*

The dorsal fields of *A. a. vulturnus* are sandy tan, lighter than in the other populations of Andros Island. The interlimb line is black-gray, lighter than in *A. a. sideroxylon,* but darker than in *A. a. behringensis* or *A. a. kingi*; the interlimb line of *A. a. vulturnus* is also the broadest

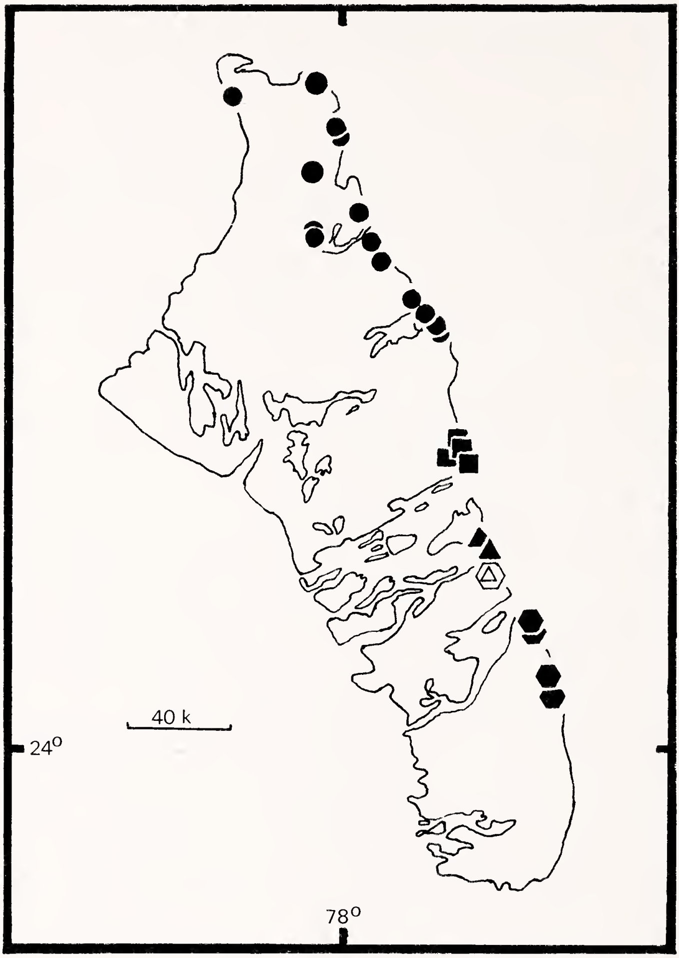

Fig. 1.—Map of Andros Island, showing localities for the subspecies of *Ameiva auberi*, as follows: solid circles = *A. a. sideroxylon*; solid squares = *A. a. behringensis*; solid triangles = *A. a. kingi*; solid hexagons = *A. a. vulturnus*. The open triangle-and-hexagon = *A. a. kingi* × *A. a. vulturnus*.

among the Andros Island subspecies. The middorsal stripe is similar to that of *A. a. behringensis* in that it is almost non-existent in males, more distinct in females. Black markings on the mesoptychium and chest of *A. a. vulturnus* extend farther posteriorly than in any other Andros *Ameiva*, in some individuals extending to the vent. The lateral fields have tan edging, the lightest edging of the *Ameiva* on Andros Island.

Etymology.—The name *vulturnus* is from the Latin meaning a southeast wind, in allusion to the southeastern range of this subspecies on Andros. The subspecific name is used as an appositional noun and thus maintains its masculine ending.

Ameiva auberi parvinsulae, new subspecies

Holotype.—CM 60542, an adult male, taken on Green Cay, Bahama Islands, on 27 December 1967 by G. A. Darling, M. W. Hucks, and J. K. Lewis. Original number ASFS V13363.

Paratypes (all from Green Cay, Bahama Islands).—ASFS V13364–69, same data as holotype; CM 41071–79, 18 July 1965, N. D. Richmond; CM 61137, 2 March 1976, A. V. Bianculli, H. K. Clench, W. T. Gillis; CM 61138–39, 2 March 1976, A. V. Bianculli.

Definition.—A Bahamian subspecies of *Ameiva auberi* occurring on Green Cay, characterized by a combination of small size (males to 85 mm, females to 66 mm SVL), moderate number of midbody granules (mean = 102.3 ± 2.6), moderate number of femoral pores (mean = 24.1 ± .61); dorsal fields brown, three dorsal lines clearly visible. Lateral fields black, with or without red edging. Snout orange; in males chin, mesoptychium, and chest to approximately the fourth ventral scale row black, with additional black patch on belly; venter blue. Tail with black lateral stripe. Juveniles vividly lined dorsally, lateral fields solid black, bordered below by white lateral stripe; throat white-gray.

Distribution.—Green Cay, Bahama Islands.

Description of holotype.—An adult male with the following measurements and counts: SVL 85 mm, tail 152 mm; GAB 106; femoral pores 11 and 12 (total 23); 30 scales in the 15th caudal verticil; fourth toe subdigital scales 35 and 37 (total 72). Dorsal fields brown, middorsal line clear, olivaceous; dorsolateral lines gray; ventrolateral line white; lateral fields black; chin, mesoptychium, and chest to the fourth row of ventral scales solid black, with black markings suffusing down blue venter to about the twenty-ninth ventral scale row.

Comparisons.—*Ameiva a. parvinsulae* is probably the smallest of the Bahamian *A. auberi* subspecies. In GAB counts, *A. a. parvinsulae* is similar to *A. a. behringensis* and *A. a. vulturnus* of Andros Island and *A. a. bilateralis* of the Ragged Islands; *A. a. parvinsulae* has lower femoral pore counts than any of the *A. auberi* subspecies of Andros Island, but almost identical to those of *A. a. bilateralis*; in 15th caudal verticil counts it is similar only to *A. a. sideroxylon*; the fourth toe subdigital counts are similar to *A. a. kingi* but closer to *A. a. multilineata* and *A. a. richmondi.*

The dorsal fields of *A. a. parvinsulae* are brown, similar to those of *A. a. bilateralis* and resembling, but not so closely, *A. a. kingi*; all three dorsal stripes are persistent, most closely resembling *A. a. multilineata*; the clear white lateral stripe is quite similar to that of *A. a. bilateralis*;

the extensive black ventral markings are also reminiscent of *A. a. multilineata.*

Etymology.—The name *parvinsulae* is from the Latin (*parva* = little; *insula* = island), in allusion to the small size of Green Cay, which is an isolated islet on the eastern margin of the Tongue of the Ocean.

DISCUSSION

The apparent land mass of Andros Island is in reality a tangled mass of smaller islands, cays, and waterways. The northern half of the "island" makes up the largest land area. It is separated from the southern land mass by a jumble of islands and channels dominated by Mangrove and Big Wood cays. The barriers these waterways present have proven sufficient to isolate at least two of the four *A. auberi* populations on Andros Island. Clench (1977) discussed the general geography and ecology of Andros in reference to butterflies and his description is equally pertinent here.

The population on Mangrove Cay is best regarded as intermediate between *A. a. kingi* and *A. a. vulturnus.* The color patterns displayed demonstrate the intermediate position of this population. Taken in sequence from south to north on Andros, the dorsal fields become progressively darker, from light tan in *A. a. vulturnus,* to a reddish tan on the Mangrove Cay specimens, to reddish tan in *A. a. kingi.* The middorsal stripe varies from pale to distinct; it is almost non-existent in *A. a. vulturnus,* becomes yellow and more prominent on Mangrove Cay, finally becomes clear and persistent on *A. a. kingi.* The interlimb line becomes progressively lighter, going from a distinct black-gray in *A. a. vulturnus,* to gray (and occasionally black) on Mangrove Cay, to hazy, very light gray in *A. a. kingi.* The black chest markings of male *A. a. vulturnus* extend well beyond the fourth row of ventral scales; on some Mangrove Cay specimens these markings are limited to the third and fourth rows, in others the black region extends well beyond these rows. In *A. a. kingi,* the black color stops at the fourth row, with occasional exceptions that extend slightly beyond.

Mangrove Cay specimens have higher scale counts than either *A. a. kingi* or *A. a. vulturnus* in all counts made. In GAB counts, Mangrove Cay specimens are similar to *A. a. vulturnus,* but have significantly higher counts than *A. a. kingi.* In both fourth toe and 15th caudal verticil counts, Mangrove Cay specimens are substantially higher than *A. a. vulturnus,* and significantly higher than *A. a. kingi* (see Table 1).

The series of specimens from Mangrove Cay is the largest sample available from Andros Island. It is possible that, with longer series of *A. a. kingi* and *A. a. vulturnus,* the Mangrove Cay series could be shown to be a distinguishable entity, but for the moment these lizards are regarded as intergrades.

The widest water channel that cuts through Andros Island separates Big Wood Cay (and the areas to the south) from the northern half of the island. It is upon this northern land mass that the other two *A. auberi* subspecies are found. There is no present obvious barrier between the known ranges of *A. a. sideroxylon* and *A. a. behringensis*; yet these two subspecies are quite distinct. *Ameiva a. behringensis* is known from only a very limited area; all specimens have been taken within a 10 km radius of Behring Point. *Ameiva a. sideroxylon,* on the other hand, has a broad distribution on the northern portion of Andros. In a general fashion, Fresh Creek separates the ranges of the two subspecies, but specimens from just *south* of Fresh Creek are *A. a. sideroxylon* and show no tendencies toward *A. a. behringensis,* as might be expected. The distance between Fresh Creek and Behring Point is about 32 km. It seems most likely that, with fluctuating sea levels, at various times Fresh Creek (or other trans-Andros bights) have been more extensive in this area, allowing *A. a. behringensis* to differentiate from its more northern relative (*A. a. sideroxylon*), and that when the present configuration of Andros Island was attained, these two northern populations maintained their identities, despite the absence (or at least reduction) of water barriers that formerly were present and were causative agents of genetic differentiation of the subspecies. *Ameiva a. sideroxylon,* on the other hand, has the broadest range of any Andros *Ameiva* subspecies; this population may be shown to be divisible into other subspecies when adequate material becomes available from the large area that northern Andros comprises.

The *A. a. parvinsulae* population is similar in various ways to all the Andros *A. auberi* populations, *A. a. multilineata* and *A. a. richmondi* (see taxonomic account of *A. a. parvinsulae*). To the other, and sometimes geographically closer *A. auberi* populations of the Bahamas, *A. a. parvinsulae* bears no significant resemblance. This is somewhat surprising because *A. a. parvinsulae* is separated from Andros Island, the Berry Islands, and the Bimini Islands by deep water but is separated from islands with other *Ameiva* populations to which it bears no resemblance (that is, *A. a. obsoleta, A. a. focalis, A. a. thoracica*) by shallow water. Despite the proximity of Green Cay to the eastern coast of Andros, it lies on the eastern arm of the U-shaped Tongue of the Ocean, and literally at the very edge of that deep trough. One would thus expect that *A. a. parvinsulae* would bear a closer resemblance to those subspecies which occur on the islands east of the Tongue and this is indeed true. Despite the dissimilarities between *A. a. parvinsulae* and the other eastern subspecies noted above, the Green Cay lizards are most similar in general pattern and coloration to another eastern subspecies, *A. a. bilateralis,* from the Ragged Islands. In summary, *A. a. parvinsulae* is one of a series of five subspecies (*thoracica* on New

Providence and Eleuthera, *focalis* on the extreme northern Exuma Cays, *obsoleta* on the southern Exuma Cays and Long Island, *bilateralis* on the Ragged Islands) on the eastern arm of the Great Bahama Bank (=east of the Tongue of the Ocean), and not closely associated with the five subspecies (*multilineata* on the Berry Islands, *sideroxylon, behringensis, kingi, vulturnus*) on the western arm. This strongly suggests that *A. a. parvinsulae* has been derived by overseas transport from the more southern *A. a. bilateralis* on the Ragged Islands, rather than from more closely adjacent Andros Island subspecies or even other subspecies on the eastern arm of the Great Bank. (We have not considered, in the above discussion, the subspecies *richmondi* from the Bimini Islands nor *felis* from Cat Island, since both are geographically remote and on their own banks.)

If one takes an overview of the twelve subspecies of *A. auberi* now known from the Bahama Islands, one interesting fact is apparent. Those subspecies that occur in the north (*richmondi, focalis, thoracica, multilineata*) are the largest, with males having SVL maxima between 109 mm and 120 mm, whereas the more southern subspecies (*vulturnus, vilateralis, parvinsulae*) reach smaller sizes (SVL 85 mm to 94 mm). Intermediate subspecies or those on isolated banks (Cat Island) are intermediate in size between these two extremes. The correlation between north = large and south = small is not perfect, however, nor would we necessarily expect it to be. But the trend is obvious. Males of the four Andros Island subspecies, *intra se,* do not show it, with southern *kingi* the largest (SVL 99 mm), followed by *behringensis* (98 mm), *vulturnus* (94 mm), and *sideroxylon* (87 mm). Many factors other than pure latitudinal distribution should be considered in such a generalization.

SPECIMENS EXAMINED

Listed below are specimens examined other than of those subspecies described in the present paper:

A. a. kingi.—Gibson Cay (CM 40915–20, ASFS V15381–84, ASFS V15386–87); Big Wood Cay (ASFS V15388–89).

A. a. kingi × *A. a. vulturnus.*—Mangrove Cay, airstrip (ASFS V15560–82): 3.2–8.0 km S airstrip (ASFS V15176–208, ASFS V15210–15, ASFS V15312, ASFS V15317–20, ASFS V15322–23, ASFS V15339–42, ASFS V14343–76).

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Buden, G. A. Darling, M. T. Felix, D. C. Fowler, M. W. Hucks, M. D. Lavrich, D. C. Leber, L. K. Lewis, J. A. Rodgers, Jr., R. Thomas, and P. F. Zell.

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ARCHAEOLOGICAL INVESTIGATIONS IN THE SHELBURNE POND LOCALITY, CHITTENDEN COUNTY, VERMONT

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Abstract

The Shelburne Pond locality in Chittenden County, Vermont, contains varied evidence of human utilization as known from 31 archaeological sites. Research reported here aims to provide a first synthesis of this evidence in correlation with a known record of changing local paleoenvironments, which documents a post-Pleistocene transition from long lasting oligotrophic to modern eutrophic conditions. As indicated by diagnostic time markers and a small number of radiocarbon dates, human utilization and occupation of the Shelburne Pond locality occurred during all currently recognized temporal subdivisions of the last 8000 years of prehistory in northeastern North America and may well have occurred before that time as well. The nature of this long term human utilization of the pond area seems to have been distinctive in comparison with other known archaeological sites and site districts in the broader Lake Champlain drainage over time. However, it now appears that the intensity of this utilization increased dramatically with the formation of the modern pond environments after about 2000 years ago.

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INTRODUCTION

The Shelburne Pond locality, Chittenden County, Vermont, has been the scene of intermittent archaeological investigations over the past 40 years. Research has been concentrated at two archaeological sites, the Ewing (VT-CH-5) and Auclair (VT-CH-3) sites (Fig. 1), which provide combined evidence of at least 8000 years of human utilization at Shelburne Pond; 29 other archaeological sites have been identified through the course of past and current research efforts. Together with Ewing and Auclair, they are the subject of consideration in this first synthesis of the prehistory of the Shelburne Pond locality.

The most general objective of the current research has been the definition of hunter-gatherer settlement and subsistence systems in a mid-latitude temperate forest, with the recognition that these systems for human adaptation are poorly known in regional (Dincauze, 1980: 30–31; Keene, 1981:171) and broader contexts (Clarke, 1979; Lee and DeVore, 1968:4–5). It should be emphasized that this research has only sampled one portion of what were undoubtedly more far ranging settlement systems, which can be reconstructed through local and regional correlation as available but incomplete data permit. Toward this end, current research has concentrated on the Ewing site, offering as it does a unique degree of organic preservation among archaeological sites with similar open, non-shell midden, interior settings in northeastern North America. In contrast to the typical situation where "preservation of bone, wood, and fiber, including faunal and floral remains is poor to nonexistent . . ." (Borstel, 1982:83), the Ewing site strata contain diverse bone, seed, and nut subsistence remains and bone and antler tools in association with varied lithic and ceramic remains as well as cultural features. This favorable degree of preservation is apparently due to neutral soil pH conditions derived from carbonate-rich dolomite bedrock backing the site.

The current research has been also designed to capitalize on Holocene paleoenvironmental research conducted in the Shelburne Pond locality since 1972 by Dr. Ian Worley and his students. Radiometrically dated pollen, diatom, and sediment studies have allowed the reconstruction of a detailed local paleoenvironmental sequence (Carr et al., 1977). These data, with other local and regional studies (for example, McDowell et al., 1971; Whitehead and Bentley, 1963), provide a basis for understanding local and regional changes in the environment in response to which human adaptations during the Holocene epoch may be assessed.

ENVIRONMENTAL SETTING

The Shelburne Pond locality is situated within the northeastern portion of North America, or the Northeast (UTM coordinates of the

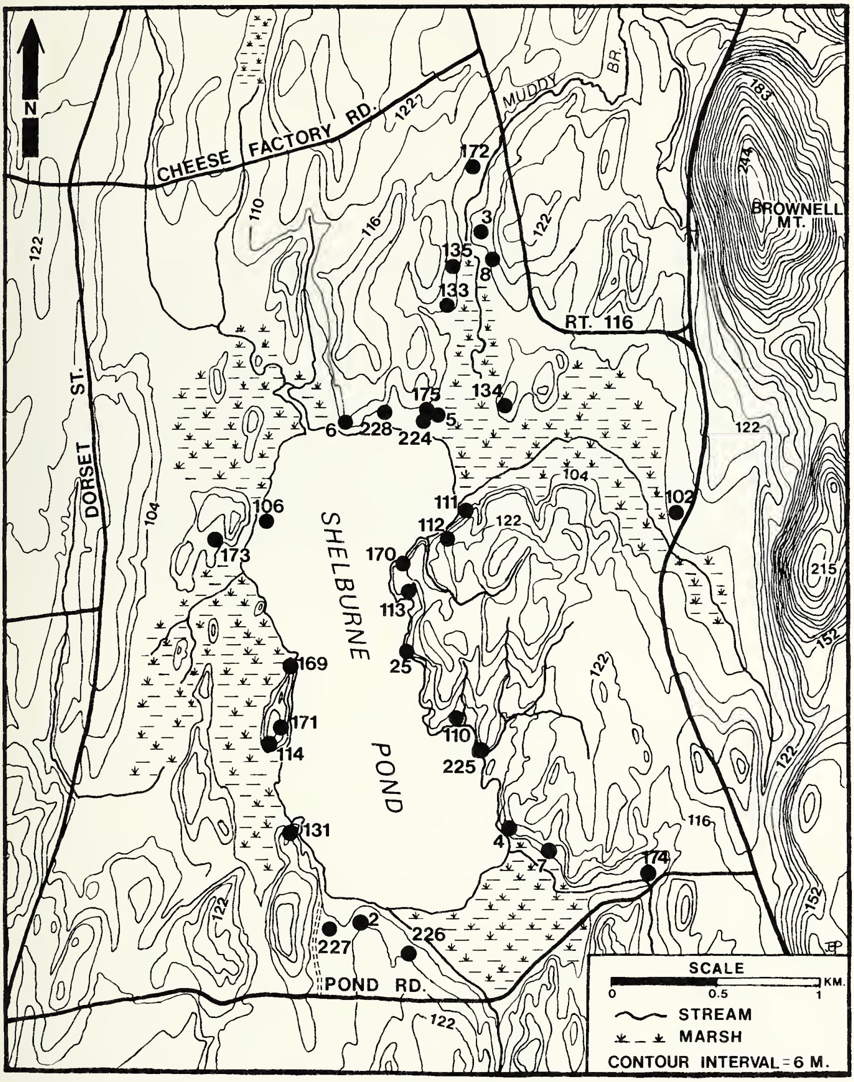

Fig. 1.—Map of the Shelburne Pond locality. Archaeological sites are labelled using numeral designations of the Vermont site inventory, Vermont Division for Historic Preservation (for example, VT-CH-3).

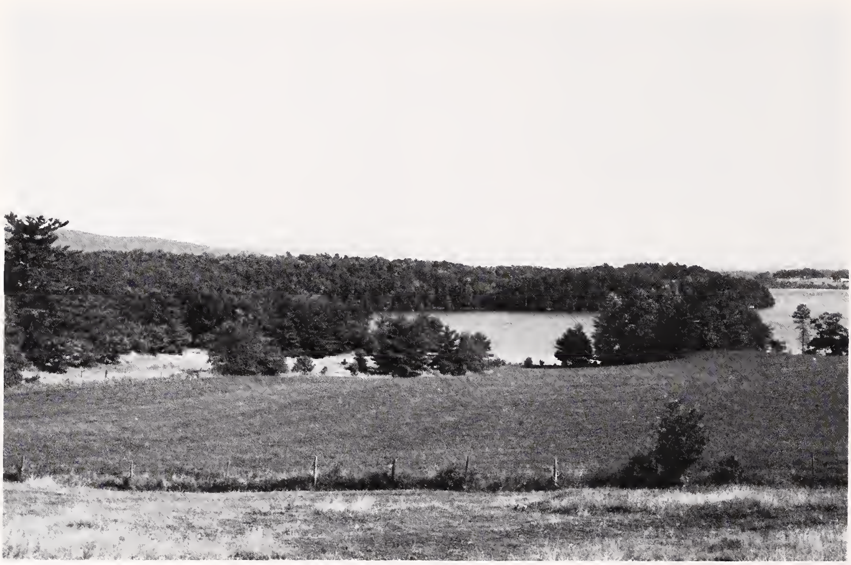

Fig. 2.—General view of Shelburne Pond facing south. The main axis of the Green Mountains is visible in the center distance. The highest visible peak is Mt. Abraham at 1221 m a.s.l. and 30 km distant.

locality are: Zone 18; NW-E646970, N4918560; NE-E646980, N4919230; SE-E648430, N4915370; SW-E643170, N4914730). Modern climatic data for nearby Burlington, Vermont, indicate a January mean temperature of 16°F, a July mean temperature of 69°F, and a yearly mean temperature of 43.2°F. Mean annual precipitation is about 84 cm (33 in), with 178 cm (70 in) of snowfall and a frost free season generally greater than 140 days (Lautzenheiser, 1974:141).

In hydrological terms, the Shelburne Pond locality lies centrally within the Lake Champlain drainage and therefore within the extensive Great Lakes-St. Lawrence River basin. More specifically, Shelburne Pond drains to the north via its only outlet, Muddy Brook, a small, meandering waterway, some nine linear kilometers to the Winooski River. The Winooski River, the largest tributary of Lake Champlain, flows to the west through the broad, low-lying Winooski Intervale, across the Champlain Lowlands physiographic region stretching to the north and south of Shelburne Pond. Lake Champlain lies only 4.6 linear kilometers to the west of Shelburne Pond at the closest point in Shelburne Bay.

The Champlain Lowlands zone is generally characterized as low country, gently rolling with broad hills, glacial lakeshore terraces and

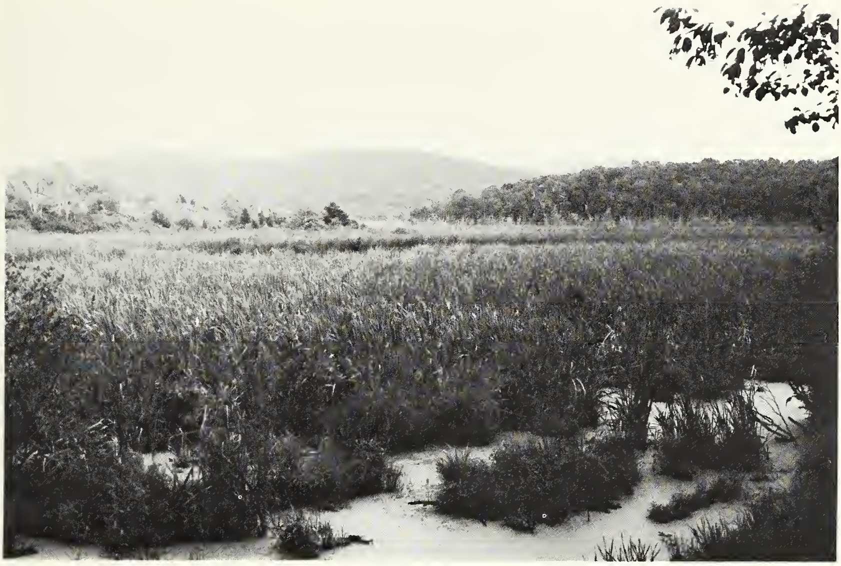

Fig. 3.—The northeast marsh of Shelburne Pond adjoining the Ewing site (VT-CH-5) facing southeast. The peak of the unnamed center hill is 214.6 m a.s.l. and about 2 km distant.

fossil delta plains. Bedrock occurs in narrow north-south trending ridges and is generally composed of metamorphosed shales, sandstones, dolomites, and limestones (Howland, 1974:10). Only 10 to 15 km to the east, the Green Mountains rise precipitously as do the Adirondacks immediately to the west on the opposite shore of Lake Champlain. The highest peaks in these mountain systems exceed 1220 m and 1524 m, respectively, whereas Lake Champlain lies at only 29 m above mean sea level (a.s.l.). The entire region was heavily glaciated during the Pleistocene epoch (Stewart and MacClintock, 1969). In broad ecological terms, the Champlain Lowlands lie within the Hardwoods White Pine-Hemlock Forest zone (Westveld et al., 1956) and the Canadian Transitional faunal zone (Briggs, 1974:52–56; see Thomas and Doherty, 1981:29–33).

Shelburne Pond is about 2.4 km long, 1.1 km wide, and covers some 179 ha (432 acres), with a local internal hydrology that drains 1628 ha (4020 acres). The pond lies within a shallow valley bounded by low hills and a long low ridge, typical of the entire Champlain Lowlands (Fig. 2). Local elevations range from 101.3 m (332 ft) a.s.l. on the pond surface to 250.1 m (820 ft) a.s.l. at the peak of nearby Brownell Mountain to the east (see Fig. 1). The north-south axis of the local valley is

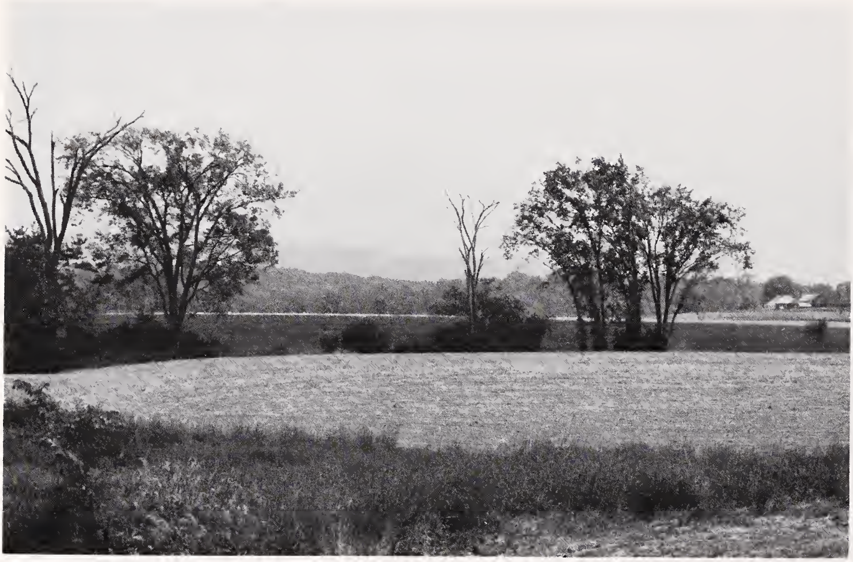

Fig. 4.—Cultivated field on the southwest shore of Shelburne Pond facing east. VT-CH-179 lies in the cultivated field and VT-CH-2 is located in the hay field behind the first tree line.

controlled by overthrust faults on the eastern pond shore and the long structural ridge on the western shore. Surficial deposits around Shelburne Pond are largely late Pleistocene lacustrine clays and silts which co-occur with glacial till over the local bedrock of Cutting dolomite, Clarendon Springs dolomite, and members of the Shelburne and Bascom formations (Doll, 1961). These deposits and the topography of the area indicate that the local drainage emerged as a separate entity after about 11,700 B.P. (9750 B.C.) with the recession of a series of late Pleistocene regional lakes, the latest of which are the Fort Ann and Greens Corners stages of glacial Lake Vermont (Carr et al., 1977; Heindel, 1980). Except where noted, all dates reported here are uncorrected.

The subsequent history of the Shelburne Pond locality witnessed the presence of a local lake, "Shelburne Lake," from about 11,700 B.P. (9750 B.C.) to about 2000–1600 B.P. (50 B.C.–A.D. 350). By A.D. 350, the major bays had infilled with extensive marshes and a true bog, present today, initiating the modern configuration of Shelburne Pond (Fig. 3). Finally, between 60 and 30 B.P. (A.D. 1890–A.D. 1920), a "marsh dam" accumulated at the pond outlet, due in part to the clearing of the land for Euro-American farmsteads with resultant silt runoff, increase in pond nutrients and marsh-building, which raised the pond

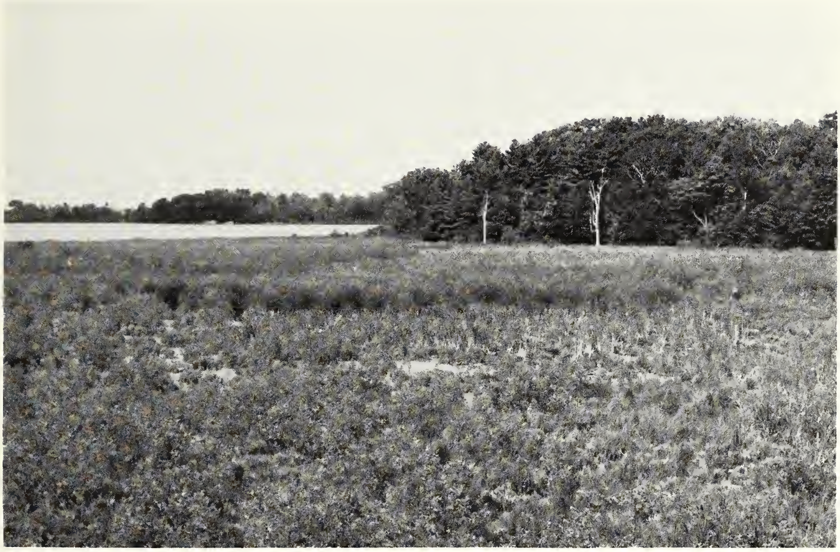

Fig. 5.—Mixed vegetation on the Ewing site facing west across the northeast marsh of Shelburne Pond (photograph taken from VT-CH-134). The Ewing site lies behind the two visible dead elms. The Adirondacks, some 62 km distant, are barely visible in the left far distance behind the open pond.

level 1.5 m to its current elevation. The modern pond is shallow and eutrophic (Carr et al., 1977:94–98).

Paleoenvironmental data derived from several cores taken from the pond reveal that aquatic life forms would have been limited before about 9500 B.P. (7550 B.C.). While varied aquatic life forms became more common after that time, it appears that aquatic productivity increased sharply only after formation of the modern pond at about 1600 B.P. (A.D. 350) (Carr et al., 1977:86–92).

Corresponding vegetation shifts are known from pollen and macrofloral remains in the Shelburne Pond cores. These reflect the early establishment of a conifer dominated forest, with pine (*Pinus* sp.) dominant after 9500 B.P. (7550 B.C.). After 7400 B.P. (5450 B.C.), hemlock (*Tsuga* sp.) and the introduction of hardwood species are documented, with a subsequent decline in hemlock. The first notable presence of aquatic plants follows 4300 B.P. (2350 B.C.). More recently, hemlock returned along with spruce and fir in the period of the local pond about 1600 B.P. (A.D. 350) (Carr et al., 1977:94–97).

The modern forest is successional and much disturbed by Euro-American occupation of the local drainage, with cultivated fields, pasture, and abandoned fields present in close proximity to the present pond (Fig. 4). Mixed hardwoods and conifer tree species are present (Fig. 5), including white cedar, hemlock, white and red pine as well as elm, maple, alder, willow, basswood, and oak species (see Borie, 1977; Lief, 1978; Siccama, 1971). Shelburne Pond is known as one of the most outstanding fish breeding grounds within the Lake Champlain drainage (J. Anderson, personal communication, 1977). Other local resources include seasonal concentrations of migratory waterfowl, as frequently observed during the current research, and a wide variety of other avian, terrestrial and aquatic resources. Much of the immediate Shelburne Pond environs is included within the H. Laurence Achilles Natural Area, which has been transferred to the University of Vermont by The Nature Conservancy as "the only large, undeveloped pond remaining in the Champlain Valley" (Borie, 1977:16; Leif, 1978). The biotic wealth and uniqueness of this area cannot be overemphasized as they certainly figured strongly in the aboriginal patterns of local exploitation.

ARCHAEOLOGICAL INVESTIGATIONS

The earliest documented archaeological research in the Shelburne Pond locality was conducted in 1941, when an "expedition," sponsored by the Vermont Historical Society (VHS) and supervised by H. Jermain Slocum, undertook excavations at two sites (Hatch, 1943). On the basis of a brief, unpublished description, one of these sites was almost certainly the Ewing site (VT-CH-5 in the modern Vermont survey files), where multicomponent deposits (that is, representing more than one usage) were removed in less than two weeks, disturbing a large area which covered some 90 to 120 m^2, or roughly 15 to 20% of the total site area. This site, "produced material classed by Ritchie as belonging to the Laurentian Aspect and consisted of a copper awl, plummet stone, pottery, arrows, several bone tools . . . and three post molds were in evidence" (Hatch, 1943:2). The archaeological deposits were apparently not screened and numerous fragments of bone, pottery, and lithic flakes are still evident in the large linear backdirt pile adjacent to this trench (Figs. 6–7). The location of the second site tested by the VHS expedition has not be ascertained, although it reportedly produced late prehistoric or "contact material," including copper beads "made from European copper," "a late Algonquin pipe," "pottery of Iroquoian characteristics" from three vessels, bone awls, and a bone projectile point (Hatch, 1943:2). Unfortunately, the collections from the 1941 VHS excavations in the Shelburne Pond locality have yet to be relocated.

Further excavation was conducted at the Ewing site by a local amateur archaeologist, one of the subsequent founders of the Vermont

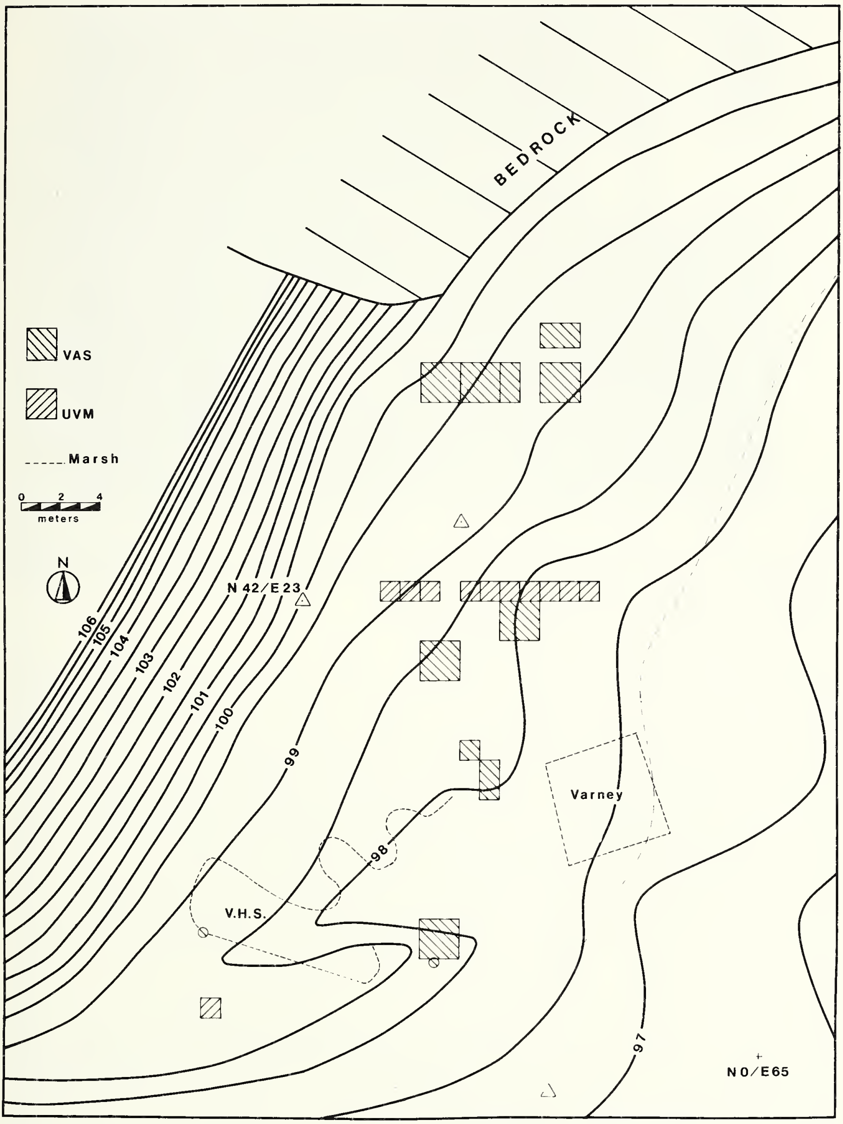

Fig. 6.—Topographic map of the Ewing site. The various excavation areas are denoted. The contour interval is 0.5 m.

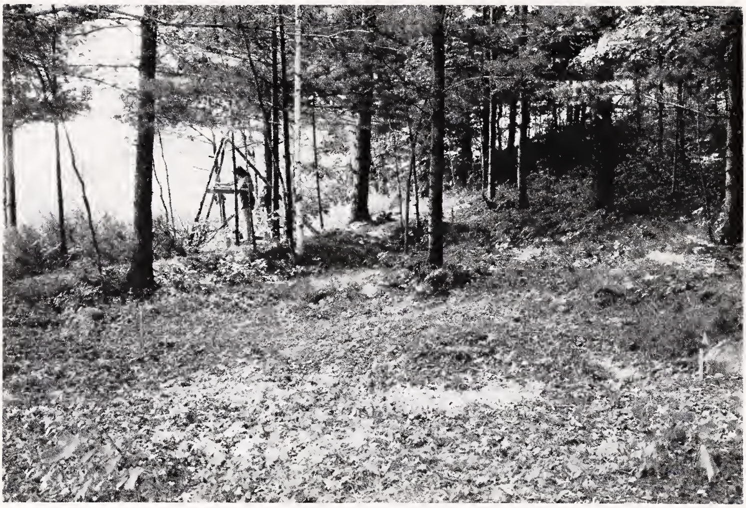

Fig. 7.—General area of the Vermont Historical Society (VHS) and Varney excavation areas at the Ewing site facing southwest. The 1983 field school excavator in left distance is standing to the north of excavation unit N3,4/E37,38 and to the south of the VHS linear backdirt pile.

Archaeological Society (VAS), Mr. Ken Varney. Intermittently between 1962 and 1967, he opened an area about 36 m^2 in size adjoining the 1941 VHS excavation (Fig. 6). Varney's excavation is considerably better documented than the earlier work, including provenience information and stratigraphic details summarized in his unpublished notes (Varney, n.d.). Varney recovered diverse cultural materials from three somewhat mixed stratigraphic layers through excavation, screening and selective retention of his collection (see Table 1 for a summary of his and later collections from the Ewing site). Prior to and during this same general period, Mr. Varney made surface collections from seven other sites around Shelburne Pond (Figs. 4, 8–9). A portion of the Varney collection from the Ewing site has been analyzed and briefly reported (Petersen, 1977, 1978), which led to the generous donation to the University of Vermont of the entire Varney collection from the Shelburne Pond locality and elsewhere.

With the formation of the Vermont Archaeological Society in 1968, this organization initiated intermittent research in the Shelburne Pond locality which has continued to the present. Excavation was first undertaken by the VAS at the Auclair site (VT-CH-3) in 1969, which is located near the outlet of Shelburne Pond on Muddy Brook across from the Ewing site (see Fig. 8). The Auclair site had been surface collected

Table 1.—*Preliminary inventory of cultural materials from Ewing site (VT-CH-5) excavations.*

Material	Varney[1]	VAS[2]	UVM[3]	Totals
Projectile point	194	149	27	370
Biface	37	73	37	147
Uniface	46	42	11	98
Modified flake	3 (?)	82	28	113 (+)
Drill	4	4	—	8
Core	?	3	7	10 (+)
Chopper	?	—	3	3 (+)
Celt	2	1	—	3
Gouge	1	—	—	1
Plummet	1	—	—	1
Net sinker	?	—	1	1 (+)
Mortar	—	1	—	1
Hammerstone	4	19	9	32
Pitted stone	1	—	—	1
Abrader	3	1	2	6
Pestle	—	1	—	1
Ground slate	1 (?)	—	—	1 (+)
Worked bone/antler	13 (?)	21	7	41 (+)
Lithic flakes	?	11,874	30,131	42,005
Fire-cracked rock	?	?	11,213 (464 kg.)	11,213
Faunal remains	500 (+?)	9728	30,761	41,489 (+)
Ceramics (sherds/fragments)	1877	1701	2360	5938
(vessels)	92 (+)	46 (+)	N.A.	139 (+)
Historic	?	7	—	7 (+)

[1] Derived from Varney (n.d.), Ritchie (1970) and Cowan (1977); screened sediment from an area about 36 m^2 and volume unknown.

[2] Derived from VAS computer printout; sediment screened with 6.40 mm (¼ in.) mesh from an area of 32 m^2 and volume of 20.95 m^3.

[3] Derived from UVM field counts; sediment screened with 3.20 mm (⅛ in.) mesh from an area of 11 m^2 and volume of 5.65 m^3.

+ Minimum estimate.

? Samples not systematically collected.

by Varney since at least 1963 after periodic cultivation and his collection still provides the bulk of material from this large, multicomponent, open site. The VAS excavation at the Auclair site, conducted until 1971, ultimately covered about 112 m^2 and produced a still largely unprocessed collection. Little associational data were recorded, however. The presence of only three (or more?) features was noted by the VAS, due largely to the extensive disturbance of historic cultivation, incorporating most cultural material into the plow zone (Anonymous, 1970; Basa, 1971).

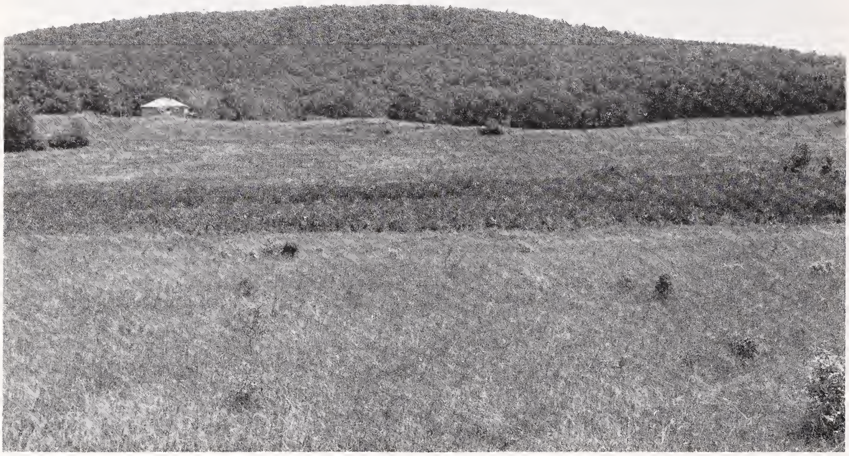

Fig. 8.—General view of Auclair I (VT-CH-3) and Auclair II (VT-CH-8) sites facing east across Muddy Brook. Auclair I is located on the intermediate terrace in the left middle foreground and Auclair II is located on the lower terrace immediately adjacent to Muddy Brook in the middle foreground. The Auclair home and Brownell Mountain are evident behind the Auclair sites. The peak of Brownell Mountain is 250.1 m a.s.l. and about 1.5 km distant.

In 1970, Dr. William A. Ritchie, then State Archaeologist of New York, conducted a brief two day reconaissance of the Shelburne Pond locality in conjunction with a broader survey of the Lake Champlain drainage after previous correspondence and consultation with Ken Varney. Ritchie's project, sponsored by the Wenner-Gren Foundation for Anthropological Research, included the study of Varney's collections from the Ewing and Auclair sites and limited testing of a few areas on the pond shore. This work ultimately led to the definition of five previously unknown sites in the Shelburne Pond locality: VT-CH-110, 111, 112, 113 and 114. The results remain unpublished (Ritchie, 1970).

The Vermont Archaeological Society returned to the Shelburne Pond locality in 1974 to undertake still another excavation attracted by the excellent conditions of preservation and the stratigraphy alluded to by Varney. This VAS excavation at the Ewing site spanned four field seasons between 1974 and 1977, first under the direction of Edgar Bacon and Louise Basa and later under Frank Cowan, ultimately uncovering some 32 m^2. Excavation was conducted in variably sized units with varying techniques to arbitrary depths; however, all deposits,

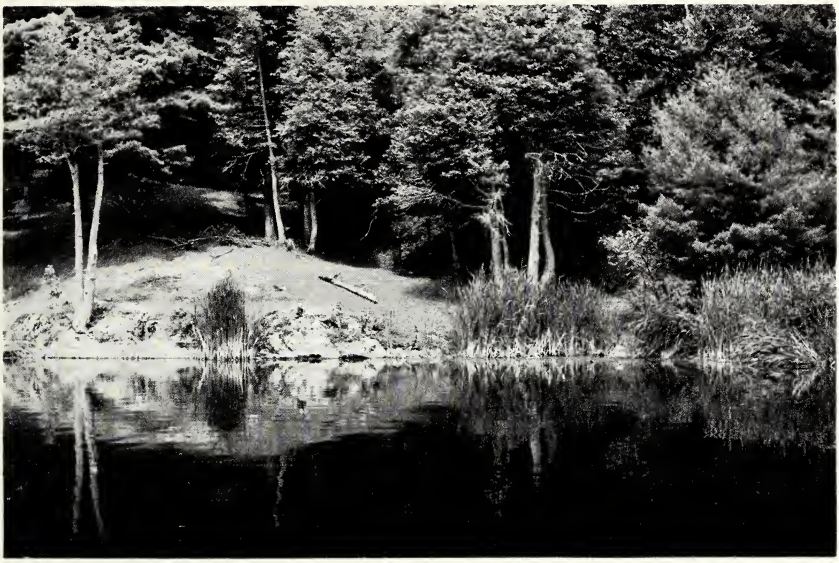

Fig. 9.—View of VT-CH-4 on the margin of the open pond and the southeast marsh of Shelburne Pond facing east.

generally removed in arbitrary 10 cm levels, were passed through 6.4 mm (¼ in) mesh screen, the first application of systematic screening at the site. This work has been briefly summarized (Bacon, 1975; Cowan, 1977), but little of the cultural material has been analyzed, with the exception of the aboriginal ceramics from the Varney and VAS collections (Petersen, 1977, 1978).

A total of what now appears to have been 13 cultural features were excavated by the VAS at the Ewing site, attributable to two (+) temporal periods. These features include surface and shallow pit hearths, at least one large roasting pit, which contained the fragmentary remains of two or three dogs, and a human burial, which was left *in situ* by the VAS. Diverse cultural materials were also recovered in and around the features (see Table 1).

A separate archaeological site, VT-CH-175, originally designated VT-CH-5A due to its proximity to the Ewing site proper, was also excavated during the 1975–1977 field seasons. The work at VT-CH-175 was undertaken by a Johnson State College field school in July and August 1975, under the direction of Louise Basa, with assistance in mapping provided by Dr. Mark Cohen and his students from SUNY at Plattsburgh. Later, this excavation was continued by members of

Table 2.—*Shelburne Pond radiocarbon dates on cultural remains.*

Location	Cultural feature	Lab no.	Years B.P.	Calendar date uncorrected	Calendar date corrected**	Material
Ewing site	VAS feature 4-76	Beta-9881	120 ± 90*	A.D. 1830	A.D. 1680–1800	charcoal
Ewing site	UVM feature 4	Beta-9880	250 ± 50	A.D. 1700	A.D. 1630	charcoal
Ewing site	UVM feature 6	Beta-9882	260 ± 90	A.D. 1690	A.D. 1530–1630	bone
Ewing site	UVM feature 7	Beta-9883	1250 ± 270	A.D. 700	A.D. 730–760	bone
Ewing site	VAS feature 1-75	Beta-9884	2715 ± 135	B.C. 765	B.C. 835–855	bone
Canoe 1	—	Beta-2501	100 ± 70*	A.D. 1850	N.A.	unburned wood
Canoe 2	—	Beta-2502	440 ± 60	A.D. 1510	A.D. 1430	unburned wood
Canoe 2	—	Beta-2706	420 ± 60	A.D. 1530	A.D. 1440	unburned wood

* Likely contaminated.

** Dendrochronological correction (Ralph et al., 1974).

the VAS, 1975–1977, who were unable to complete some of the units opened by the field school. Ultimately, a total of about 13 m^2 were excavated at VT-CH-175.

More recently, cooperative efforts of the VAS, the University of Vermont (UVM) Department of Anthropology, and the Vermont Division for Historic Preservation have recovered two partially intact dugout canoes and studied a third dugout canoe from Shelburne Pond. Two of these canoes, recovered in 1978 and 1979, were found close to aboriginal archaeological sites along the eroding shoreline. At least one of the canoes is attributable to the late prehistoric period on the basis of two radiocarbon dates kindly supported by Dr. Ian Worley–A.D. 1510 ± 60 and A.D. 1530 ± 60 (see Table 2 for these and all other available radiocarbon dates for cultural remains from Shelburne Pond). A second canoe, which may have been contaminated by preservative treatment, was dated to A.D. 1850 ± 70. The third canoe was first discovered in 1982, could not be found during 1983, but has since been relocated and left in the pond until curation problems can be dealt with in the future.

Subsequent to completion of the various VAS field projects near Shelburne Pond, a group of trained volunteers from the VAS completed processing and initial cataloging of all cultural materials recovered from the main locus at the Ewing site (VT-CH-5). All materials were coded for computer by the VAS to facilitate ultimate data manipulation. This same group of dedicated volunteers has recently begun comparable processing and cataloging for the VAS collection from VT-CH-175.

Planning for the current research project was initiated in 1981 by the University of Vermont Department of Anthropology, and the senior author, principal investigator of the 1983 Ewing site reinvestigation. A synthetic project was envisioned with the following goals: (1) limited field work to insure systematic recovery of samples, including but not limited to fine-grained material culture, subsistence, soil, and contextual data; (2) varied analyses conducted by specialists using all past samples and those to be collected from the Ewing site and other sites around Shelburne Pond, with particular attention given to chronology, subsistence and settlement; and (3) report preparation and correlation of all data from the Shelburne Pond locality within the context of local and regional prehistoric cultural systems. The present study represents the first report of what will ultimately be a complete treatment of all aspects of aboriginal usage of Shelburne Pond (for example, Adovasio, 1982; Thomas, 1983*a*, 1983*b*).

In light of these goals, the UVM Department of Anthropology conducted a reinvestigation of the Ewing site in July and August 1983, as a summer field school in archaeology (Fig. 10; Petersen, 1983). This

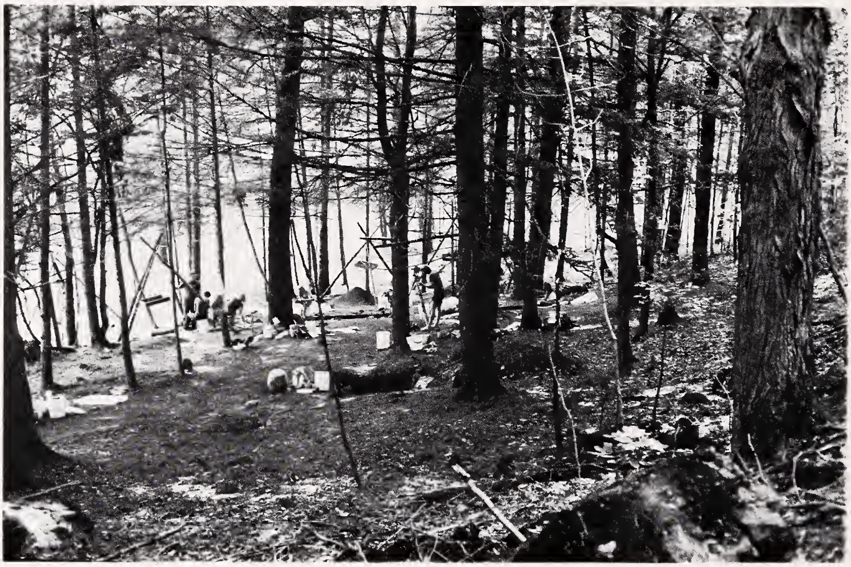

Fig. 10.—Overview of the entire Ewing site (VT-CH-5) facing south. The northeast marsh is located behind the site to the east and south. Dolomite bedrock lies in the foreground and beyond the right margin to the west of the site.

reinvestigation was undertaken in conjunction with a broader, concurrent intensive site survey within the Shelburne Pond locality. Volunteers from the VAS and the public at large also participated in the Ewing site reinvestigation.

All excavation, whether conducted by the 20 students or various volunteers, employed a standardized, systematic methodology (for example, Adovasio, 1982; Thomas and Robinson, 1983). Excavation units, each 1 m^2 and subdivided into 25 cm blocks, were arranged to provide a cross-section of the Ewing site from the sloping foot of the bedrock-controlled western margin to the marsh margin on the east. Excavation proceeded within natural strata first and foremost, using 5 cm arbitrary levels within natural strata tied to one site elevational datum point. All sediment was removed with sharpened hand-held trowels or smaller implements and passed through 3.20 mm (1/8 in) screens. Horizontal control was maintained through usage of the previously established VAS metric grid. Vertical elevations of all surfaces, strata, features, various artifacts and arbitrary levels were recorded with a transit (Fig. 11).

Extensive notes and field counts were recorded for each 25 cm subunit within each 5 cm (or smaller) level in the 1 m^2 units. All samples

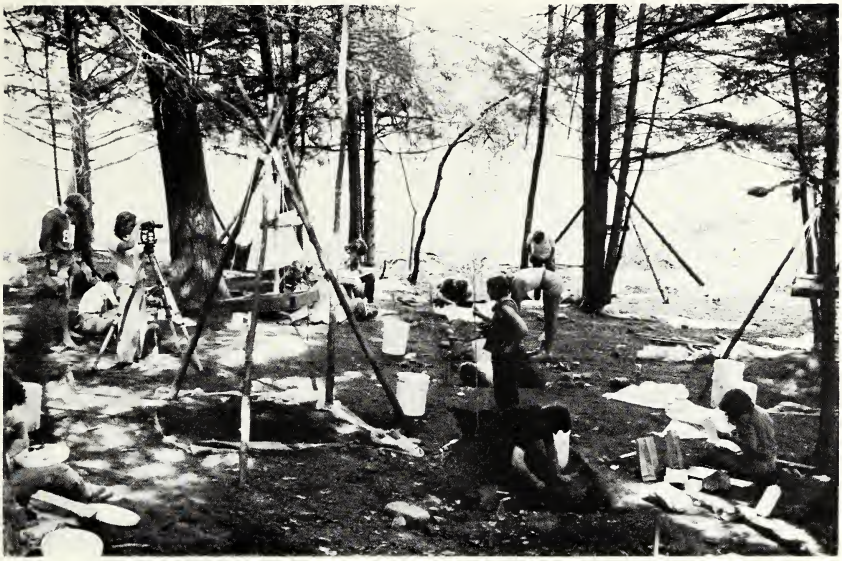

Fig. 11.—Overview of the 1983 UVM cross section trench (N23,24/E46,57) at the Ewing site facing east towards the northeast marsh.

were coded for computer in the field to facilitate later data manipulation. All feature fill was retained for flotation processing, except in a few cases where the large size of a feature necessitated sampling of its fill. Five complete 10 cm^2 column samples were collected to provide additional analyses currently underway (for example, sediment size and composition, pollen). Finally, numerous plan and cross-section profile drawings were recorded as were both color and black-and-white photographs, providing more extensive documentation.

A numerous and wide variety of prehistoric materials, some 75,000 (+) artifacts were recovered from the small but productive 11 m^2 area opened in the 1983 UVM Ewing site excavation (see Table 1). These remains included nine cultural features and a range of cultural materials similar to the Varney and VAS samples from the site, including lithic tools and debitage (waste flakes), ceramics, native copper tool fragments, bone and antler tools, some floral remains, and numerous well preserved faunal remains and associated fire-cracked (stone boiling) rocks (Fig. 12). This large quantity of cultural material is striking in comparison with samples previously obtained from the Ewing site and obviously reveals the importance of using fine-mesh screen at rich sites such as Ewing (see Starbuck, 1982; Thomas and Robinson, 1983).

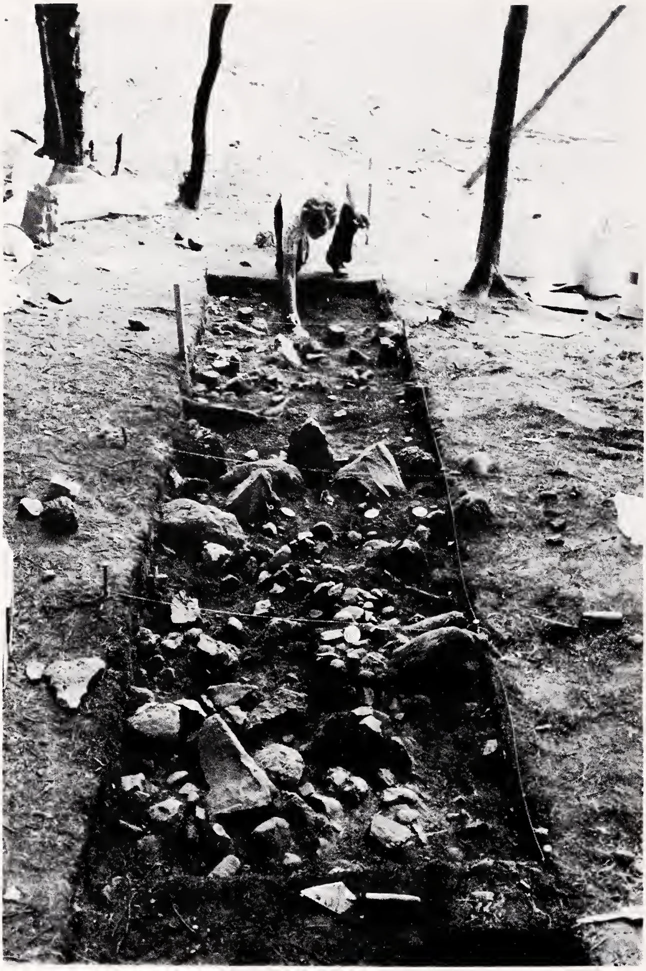

Fig. 12.—1983 UVM feature 4 fire-cracked rock and UVM feature 6 bone concentration (to left of figure) at the Ewing site facing east. This portion of feature 4 is located in trench section N23,24/E51,57 in stratum IV and is attributable to the Late Woodland and Contact periods. A 25 cm² subunit is evident immediately to the right of the hand trowel in the foreground. Two available radiocarbon dates for these features include A.D. 1690 ± 90 (bone) and A.D. 1700 ± 50 (charcoal). Both dates are uncorrected (see Table 2).

Moreover, the systematic recording and recovery of previously neglected materials, notably over 450 kg of fire-cracked rock, reveals an important new dimension for interpreting prehistoric usage and occupation there. Diagnostic artifacts from the UVM excavation and previous collections from the Ewing site provide evidence of at least six different periods of aboriginal occupation, the details of which are treated below. In addition, the Vermont Division for Historic Preservation kindly provided funding to support the radiocarbon dating of five samples from the VAS and UVM excavations at the Ewing site, which have helped in establishing an absolute chronology there (see Table 2).

The Shelburne Pond intensive site survey was undertaken to provide as detailed information as could be obtained for the other archaeological sites in the area. A secondary goal was nomination of the entire locality to the National Register of Historic Places as an archaeological district, a measure undertaken to insure federal protection of these important cultural resources in perpetuity. All 21 previously known archaeological sites in the locality were relocated on the ground, photographed, and in a few cases tested through test pits and/or auger cores. Although the goals of the site survey as set by the Vermont Division for Historic Preservation did not include location of previously unknown sites, an additional 11 sites were also identified or subdivided from within the existing site inventory during the course of field work within the Shelburne Pond locality. As seen in Table 3, the 1983 inventory from most of these sites is intentionally limited following the dictates of the Vermont Division for Historic Preservation.

SITE DISTRIBUTION AND CONTENT

The existing inventory of archaeological sites is clearly uneven, with the large bulk of cultural material and ancillary samples of environmental data derived from only a few of the 31 recorded sites in the Shelburne Pond locality. This situation is compounded by the nature of site discovery since only a core portion of the entire locality has been exhaustively surveyed and a smaller portion yet has been subsurface tested. Nonetheless, it seems equally evident that the presence of 31 archaeological sites in the most optimal settings of such a relatively small area permits and, in fact, requires some consideration of where the sites are situated and what factors possibly account for their distribution, however incomplete the inventory (Table 4).

The most striking attribute of the available sample is the near uniform proximity (distance and elevation) in relation to the existing shoreline of the pond or the past shoreline before 1600 B.P. (A.D. 350) when the various bays had yet to be infilled with marsh. The few exceptions to this pattern are sites which are situated in a similar position vis-à-vis Muddy Brook or the unnamed tributary to the southeast of Shelburne Pond; however, they are equivalent in their proximity to water. No clear correlation of site location and any of the marshes can be noted; instead, it appears that sites were more typically situated

Table 3.—*Cultural material recorded by the 1983 Shelburne Pond site survey.*

Designation (name)	Projectile points	Bifaces	Unifaces	Lithic flakes	Ground stone	Bone elements	Ceramics	Modern-historic	Fire-cracked rocks	Notes
VT-CH-2	—	—	—	15*	—	—	—	—	—	
VT-CH-3 (Auclair I)	—	—	—	—	—	—	—	—	—	Surface collection attempted—no artifacts
VT-CH-4	—	—	—	16*	—	—	—	—	—	
VT-CH-5 (Ewing)	—	—	—	—	—	—	—	—	—	
VT-CH-6	—	1	1	77	—	—	—	1	—	Four test pits excavated
VT-CH-7	—	1 core	—	867	—	—	—	28	18	One test pit excavated
VT-CH-8 (Auclair II)	—	—	—	—	—	—	—	—	—	Surface collection attempted—no artifacts
VT-CH-25	—	1 core	—	1 7*	—	—	—	—	—	Four test pits excavated
VT-CH-102	—	—	—	—	—	—	—	—	—	Surface collection attempted—no artifacts
VT-CH-106	—	—	—	102	—	327	178	12	3	Two test pits excavated
VT-CH-110	—	—	—	9	—	1	—	1	—	
VT-CH-111	—	—	—	—	—	—	—	—	—	Surface collection attempted—no artifacts
VT-CH-112	—	—	—	—	—	—	—	—	—	Surface collection attempted—no artifacts
VT-CH-113	—	3	—	43	—	—	—	1	—	Three test pits excavated
VT-CH-114	—	—	—	—	—	—	—	—	—	Surface collection attempted—no artifacts
VT-CH-131	—	—	—	—	—	—	—	—	—	Surface collection attempted—no artifacts

Table 3.—*Continued.*

Designation (name)	Projectile points	Bifaces	Unifaces	Lithic flakes	Ground stone	Bone elements	Ceramics	Modern-historic	Fire-cracked rocks	Notes
VT-CH-133	—	—	—	—	—	—	—	—	—	Surface collection attempted—no artifacts
VT-CH-134	—	—	—	2	—	—	—	—	—	
VT-CH-135	—	—	—	—	—	—	—	—	—	Surface collection attempted—no artifacts
VT-CH-169	—	—	—	34	—	4	—	1	—	One test pit excavated
VT-CH-170	—	—	—	4*	—	—	—	—	—	
VT-CH-171	—	—	—	3*	—	—	—	—	—	
VT-CH-172	—	—	—	11*	—	—	—	—	—	
VT-CH-173	—	—	—	3*	—	—	—	—	—	Two test pits excavated
VT-CH-174	—	—	—	—	—	—	—	—	—	Corn crop—not available for surface collection
VT-CH-175 (VT-CH-5A)	—	—	—	—	—	—	—	—	—	
VT-CH-224 (VT-CH-5B)	—	—	—	—	—	—	—	—	—	
VT-CH-225	—	—	2	30*	—	—	—	—	—	
VT-CH-226	—	—	—	—	—	—	—	—	—	Surface collection attempted—no artifacts
VT-CH-227	1	—	1	5 224*	—	—	—	—	—	
VT-CH-228	—	—	—	—	—	—	—	—	—	

*Observed, but not collected.

Table 4.—*Archaeological site attributes in the Shelburne Pond locality.*

Site survey designation (name)	Archaeological site attributes							
	Elevation (m)		Slope (%)	Slope direction	Distance to water (m)	Current vegetation cover/usage	Soil type (USDA 1974)	Occupied area (m²)
	a.s.l.	a.water						
VT-CH-2	109	8	0–10	N	10	cultivated field	VeB	1850
VT-CH-3 (Auclair I)	104–106	3–5	0–10	W	1–2	cultivated field	VeB/VeD	2500
VT-CH-4	101.5–103.5	0–2	10–20	SW	1–2	pasture	FaE	300
VT-CH-5 (Ewing)	101.5–103.5	0–2	10–20	E	0	conifer-deciduous	FaC	600
VT-CH-6	104–106	3–5	0–10	SW	1–2	cultivated field-pasture	VeC	880
VT-CH-7	102	1	0–10	SW	1	pasture	FaE	750
VT-CH-8 (Auclair II)	102	1	0–10	W	1	cultivated field	VeB	?
VT-CH-25	103–106	2–5	0–10	S	2	conifer-deciduous	FaE	22
VT-CH-102	106–107	5–6	0–10	W	100	cultivated field	VeB	900
VT-CH-106	102–103	1–2	0–10	NE	0	light conifer	bedrock	10
VT-CH-110	103	2	0–10	S	0	conifer-pasture	VeB	1500
VT-CH-111	103	2	0–10	NW	1	conifer	FaE	? (small)
VT-CH-112	114	13	10–20	NW	5–10	conifer	FaE	600
VT-CH-113	103	2	0–10	S	0–2	conifer-pasture	FaE	600 (?)

Table 4.—*Continued.*

Site survey designation (name)	Archaeological site attributes							
	Elevation (m)		Slope (%)	Slope direction	Distance to water (m)	Current vegetation cover/usage	Soil type (USDA 1974)	Occupied area (m^2)
	a.s.l.	a.water						
VT-CH-114	112–114	11–13	10–20	S	80	conifer-deciduous	FaE	525 (?)
VT-CH-131	113–126	12–25	20–30	N	10–20	conifer-deciduous	FaE	442
VT-CH-133	107	6	0–10	E	30–40	conifer-pasture	VeB	?
VT-CH-134	110	9	10–20	W	100	deciduous	FaC/bedrock	300
VT-CH-135	109	8	0–10	E	3–5	conifer-pasture	VeB	800
VT-CH-169	104	3	30–40	E	0–1	conifer	FaE	42
VT-CH-170	107	6	0–10	NW	5	conifer	FaE	24
VT-CH-171	104	3	10–20	E	3–5	conifer	FaE/bedrock	200–300
VT-CH-172	105–106	4–5	10–20	E	10–12	cultivated field	VeD	60
VT-CH-173	106	5	0–10	SE	100–150	deciduous-conifer	VeB	35
VT-CH-174	113–114	12–13	0–10	S	50–60	pasture	VeB	1200
VT-CH-175 (5A)	113	12	0–10	S	15	conifer-deciduous	FaC	300–400
VT-CH-224 (5B)	109–110	8–9	0–10	S	10	conifer	FaC	100
VT-CH-225	116–121	15–20	10–20	SW	3–5	conifer	FaC/bedrock	45
VT-CH-226	109	8	0–10	NE	30	cultivated field	VeB	3000
VT-CH-227	104–111	3–10	0–10	N	3–5	cultivated field	VeB	2000
VT-CH-228	104–105	3–4	0–10	S	25	conifer-pasture	VeC	? (small)

Table 5.—*Cultural components represented in the Shelburne Pond locality by archaeological site and temporal period.*

	Temporal period							
		Archaic			Woodland			
	Paleo-indian	Early	Middle	Late	Early	Middle	Late	
Site survey designation (name)	?–7000 B.C.	7000–6000 B.C.	6000–4000 B.C.	4000–1000 B.C.	1000–100 B.C.	100 B.C.–1000 A.D.	A.D. 1000–1700	Unknown prehistoric
VT-CH-2	—	—	—	*	—	*	*	—
VT-CH-3 (Auclair I)	*?	*	*	*	*	*	*	—
VT-CH-4	—	—	—	*?	—	—	*	—
VT-CH-5 (Ewing)	—	*	—	*	—	*	*	—
VT-CH-6	—	—	—	*	*	—	*	—
VT-CH-7	—	—	—	*	—	—	—	—
VT-CH-8 (Auclair II)	—	*	—	*	—	—	*	—
VT-CH-25	—	—	—	*	—	—	*	—
VT-CH-102	—	—	—	—	—	—	—	*
VT-CH-106	—	—	—	—	—	*	*?	—
VT-CH-110	—	—	—	—	—	—	*	—
VT-CH-111	—	—	—	—	—	—	—	*
VT-CH-112	—	—	—	—	—	—	—	*
VT-CH-113	—	—	—	—	—	—	—	*
VT-CH-114	—	—	—	*	—	—	—	—
VT-CH-131	—	—	—	—	—	—	*	—
VT-CH-133	—	—	—	—	—	—	*	—
VT-CH-134	—	—	—	*	—	—	—	—

Table 5.—*Continued.*

Site survey designation (name)	Temporal period							
	Paleo-indian	Archaic			Woodland			Unknown prehistoric
		Early	Middle	Late	Early	Middle	Late	
	?–7000 B.C.	7000–6000 B.C.	6000–4000 B.C.	4000–1000 B.C.	1000–100 B.C.	100 B.C.–1000 A.D.	A.D. 1000–1700	
VT-CH-135	—	—	—	—	—	—	—	*
VT-CH-169	—	—	—	—	—	—	—	*
VT-CH-170	—	—	—	—	—	—	—	*
VT-CH-171	—	—	—	—	—	—	—	*
VT-CH-172	—	—	—	—	—	—	—	*
VT-CH-173	—	—	—	—	—	—	—	*
VT-CH-174	—	—	—	—	—	—	—	*
VT-CH-175 (VT-CH-5A)	—	—	—	*	—	*	*	—
VT-CH-224 (VT-CH-5B)	—	—	—	—	—	—	*	—
VT-CH-225	—	—	—	—	—	—	—	*
VT-CH-226	—	—	—	—	—	*	*	—
VT-CH-227	—	—	—	—	—	—	*	—
VT-CH-228	—	—	—	—	—	—	—	*
Frequency	1	3	1	11	2	6	14	13
Raw percentage	(2.6%)	(7.7%)	(2.6%)	(28.2%)	(5.1%)	(15.4%)	(35.9%)	(42.0%)
Ratio (components/100 years)	N.A.	0.30	0.05	0.37	0.22	0.55	2.00	

adjacent to what is today open water (for example, Fig. 9). This latter observation may be merely a condition of site survey and sampling, however, and necessitates further testing through future research. In any case, the location of sites in comfortable proximity to surface water is not at all surprising, having been noted in many other studies of broader scale (for example, Hamilton et al., 1984; Roll and Smith, 1982; Thomas and Bettinger, 1976). Exceptions to this principle are largely dictated by other special value resources, such as lithic raw materials or game procurement.

Other site attributes, which similarly offer no surprises, include the level to slightly sloping character of modern site surfaces and the association with rocky, well drained soils of the Farmington series or better drained clays of the Vergennes series in preference to less well drained soils. Slope direction does not appear to have been a first priority attribute in site selection, at least in comparison with the aforementioned attributes, since site slope directions are present in all of the eight orientation categories employed here. Only ca. 25% of the sites slope northward (N, NE or NW), as contrasted with some 42% which slope southward (S, SE or SW). This differential distribution may tentatively reflect a southerly facing preference to optimize solar radiation and/or the local northerly winds, which still moderate potential insect pests at sites such as Ewing and VT-CH-6.

Little can be inferred from the presence of modern vegetation types other than the general correlation of specific plant species (inventoried, but not mentioned here), with the varying drainage conditions in the study area. Changing environmental conditions and the impact of historic Euro-American occupation have radically transformed the nature of the vegetation cover.

Estimates of site size were derived from accumulated knowledge (Varney, VAS, and UVM) of surface and subsurface distribution of cultural materials. Although tentative, or unknown in some instances, it is evident that most of the sites in the Shelburne Pond locality are small in overall size in spite of the fact that a number were clearly the product of repeated visits for different purposes. With a few exceptions (for example, VT-CH-2, VT-CH-3), site size appears to be constrained by potentially usable space and the nature of the specific activities which were conducted.

The available distribution of site components by temporal period has been determined on the basis of diagnostic time markers, largely projectile points and to a lesser degree, ceramics. These time markers reflect increasing utilization of the area over time based simply on the changing percentages of components represented in any one period relative to the total number of known components (n = 39) in the study area (Table 5). The Late Archaic and Late Woodland periods appear, on first consideration, to represent the two peaks of a bimodal distribution. However, comparison of adjusted ratios for the number of components per 100 years of duration reveals a smooth unimodal peak in the Late Woodland period. This is closer to a true index of utilization over time. This assessment assumes representativeness of the available sample, however, which can not be conclusively demonstrated. Some 42% (n = 13) of all sites in the Shelburne Pond locality can not be assigned to any specific temporal period and additional components may well remain to be identified at the other sites.

CULTURAL CHRONOLOGY

Human utilization of the Shelburne Pond locality has minimally spanned some 8000 years and quite probably exceeded 9000–10,000 years in duration. Although few absolute dates are yet available to corroborate this sequence, stratigraphic information from the Ewing site and diagnostic artifacts from the Ewing, Auclair, and other sites, enable tentative identification of a series of sequent periods of utilization and probable occupation. In point of fact, no other locality within the entire Lake Champlain drainage basin or the State of Vermont provides such a relatively complete sequence in such a relatively small area. The data available from the several investigations are significant and have been described in some detail here, including a discussion of the stratigraphy and periods of occupation at the Ewing site as well as a summary of known usage of the entire Shelburne Pond locality.

Stratigraphic information from the Ewing site has been compiled from the three most recent phases of investigation at the Ewing site (Varney, VAS, and UVM excavations). Correlation of the available accounts reveals apparently varying degress of stratigraphic complexity in the soil, classified as Farmington extremely rocky loam (FaC), with a 5 to 20% slope (Allen, 1974: Sheet 45). Deeper, more varied stratigraphy has been noted in the southeastern portion of the site excavated by the VHS and Mr. Ken Varney (Table 6).

Detailed stratigraphic data were accumulated by the 1983 UVM reinvestigation of the Ewing site, with a master profile produced for the VAS and UVM excavations (see Table 6; Fig. 13). In essence, excavations document the post-Pleistocene building of sediments at the Ewing site largely through colluviation (slope wash) and organic decomposition above late Pleistocene lacustrine deposits left by the final Fort Ann and Greens Corners stages of glacial Lake Vermont. The top of the late Pleistocene (ca. 11,700–12,000 B.P.) sediment deposit is about 70 cm below modern ground surface (Varney excavation)

Table 6.—*Recorded stratigraphic profiles for Ewing site (VT-CH-5).*

1983 stratum	Soil horizon	Generalized profile for the Varney excavation (from Varney, n.d.) depth (cm below surface)	Description
IV	A	0–20	"very black soil, pH of over 7.0"
IIIb (?)	B_1 (?)	20–36	"brownish to reddish-brown color (soil) and contains considerable stone"
IIIa (?)	B_2 (?)	36–71	"blackish in color, pH above 7.0 and relatively stone-free"
II	C_1	71–?	"white-grey, marl-like, sterile soil"

1983 stratum	Soil horizon	Master profile for UVM and VAS excavations (N35.32/E51–52) depth (cm below surface)	Description
IV	Aa	0–22	Dark grayish brown, Munsell 2.5Y 4/2; silt loam; medium structureless crumb; very friable; non-plastic; few medium roots; pH 6.8; moisture 25%; clear smooth boundary; 10–22 cm thick.
III	B	22–48	Light yellowish brown, Munsell 2.5Y 6/4; sandy silt; fine structureless granular; soft; non-plastic; few fine roots; pH 7.0; moisture less than 5%; gradual wavy boundary; 22–35 cm thick.
II	C_1	48–80	Olive yellow, Munsell 2.5Y 6/6; sandy silt; fine structureless granular; very friable; non-plastic; very few fine roots; pH 6.9; moisture 15%; clear smooth boundary; 26–42 cm thick.
I	C2x	80–110	Light yellowish brown, Munsell 10YR 6/4; sandy silt with cobbles; very fine structureless granular; very firm, compact, weakly cemented fragipan; some cobbles in an ill defined layer; pyrolucite (MnO_2) on lower surface of cobbles; non-plastic; no roots; pH 7.0; moisture 20%; lower boundary not seen.

at the deepest and elsewhere ranges from 28 cm to 48 cm below modern ground surface (VAS and UVM excavations). The nature of the sediment deposition, soil development and occupational and post-occupational disturbances renders precise separation of different aboriginal occupations impossible (for example, Stein, 1983; Thomas and Robinson, 1983; Villa and Courtin, 1983:271–272). Nonetheless, the available stratigraphic information does allow documentation of peaks of occurrence for cultural material in the natural stratigraphy as well as some horizontal separation of noncontemporaneous deposits. The depositional status of VT-CH-5 is no different and often better than the majority of archaeological sites outside of floodplains or other actively building depositional environments in the broad Northeast (for example, Borstel, 1982:13–16; Funk, 1976:10–11, 23; Spiess and Hedden, 1983:27–54; Starbuck, 1982:7–8). In sum, the relatively shallow nature of the post-Pleistocene stratigraphy, while better than most or all other sites in the Shelburne Pond locality, will allow tentative separation only of the different episodes of utilization and occupation, here referred to as components (see Willey and Phillips [1958] for archaeological terminology).

The earliest utilization of the Ewing site is ascribable to the Early Archaic period (Thomas and Robinson, 1983), ca. 6100 B.C., on the basis of a single projectile point (Fig. 14a). This point from the Ewing site, named the Swanton corner notched type by Thomas and Robinson (1983:57–62; Plate 1), was among the deepest (61 cm below surface) finds in stratum IIIa in the Varney excavation (Varney, n.d.). Swanton corner-notched points are best known and dated at the John's Bridge site (VT-FR-69) on the Missisquoi River in northwestern Vermont. A small number of other such finds are known in the Lake Champlain drainage, including specimens from the Auclair site (Thomas and Robinson, 1983:127–129).

The first well represented components at the Ewing site occur much later during the Archaic period. Comparative projectile points and a variety of other diagnostic tools indicate several components ascribable to the "Laurentian" tradition of the Late Archaic period, ca. 3500 B.C.–2500 B.C. (Funk, 1976:235–246; Ritchie, 1965:79–125; Ritchie and Funk, 1973:37–51, 339–341). We have relied on New York State terminology here as convenient labels for what seem to be discrete periods of prehistory. These periods have been defined on the basis of long term research conducted by William Ritchie, Robert Funk and others and through their usage we only mean to imply rough contemporaneity rather than precise correspondence. Where local data permit, however, we have employed new terminology to label local developments. In any case, the earliest component at the Ewing site of what has been elsewhere labelled the "Laurentian" tradition is represented by a small inventory of Vergennes phase Otter Creek points (Fig. 14b, c, h), generally from Ewing stratum III, and other tool forms which likely date from before 3000 B.C. The Vergennes phase is also known from the Otter Creek No. 2, KI and other sites in the Lake Champlain drainage (Ritchie, 1965:84–89, 1968, 1979; see also Bailey, 1939*a*; Funk, 1976:233–235; Funk and Hoagland, 1972).

The immediately sequent Ewing phase (as first named here), a Vosburg-like complex, represents the predominant "Laurentian" occupation at the Ewing site, ca. 3000–2500 B.C. (see Funk, 1976:239–

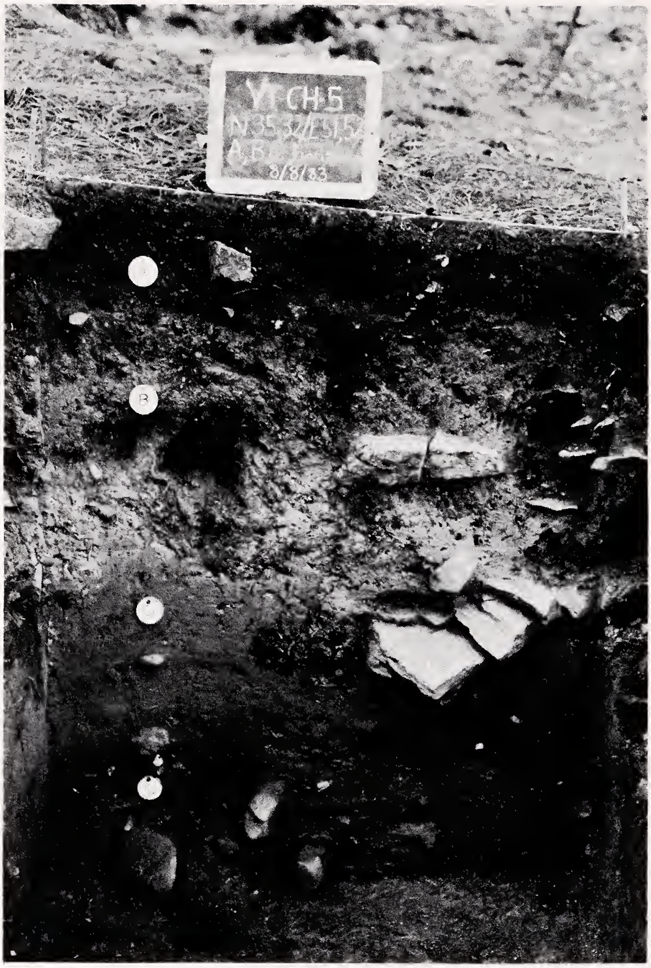

Fig. 13.—Master profile for the VHS and UVM excavations at the Ewing site facing north (see Table 6 for detailed strata descriptions).

246). Characteristic Vosburg points (Fig. 14d–g, i–k) are attributable to the stratum III Ewing phase component and some combination of native copper tools (Fig. 15), a plummet and a gouge (Fig. 16), bifaces, pitted stones, other stone tools, at least several bone and antler tools and fire-cracked rock and hearth features (Fig. 17). The Weinman site on Lake George (Funk, 1976:20–21), Sylvan Lake Rockshelter (Funk, 1976:156–167) and the Ten Mile Rockshelter (Funk et al., 1971) doc-

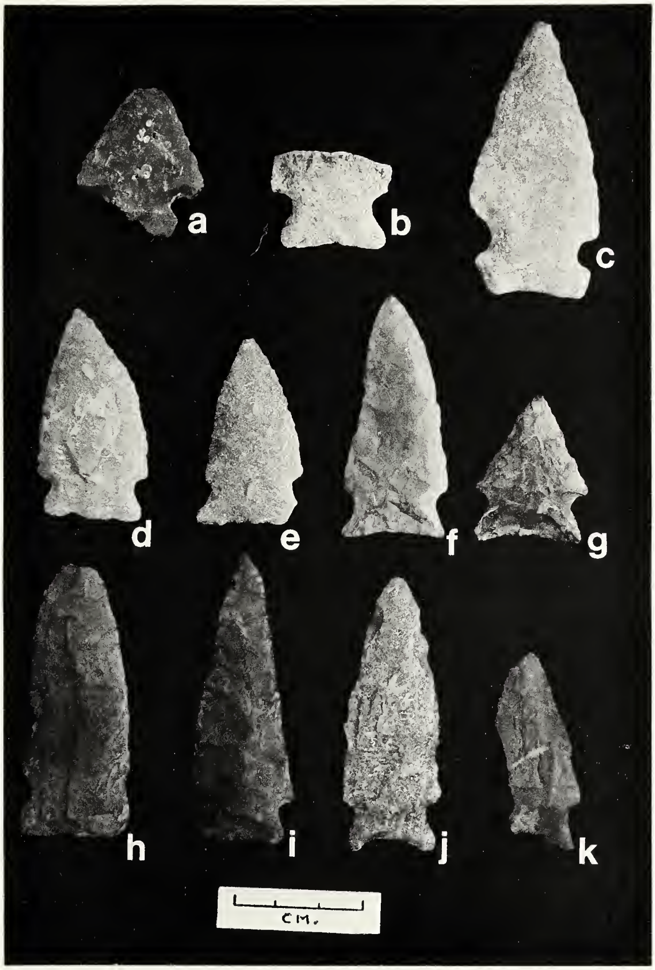

Fig. 14.—Early Archaic and Late Archaic period projectile points from the Ewing site: a is a Swanton corner notched point; b, c, h are Otter Creek points; d–g, i–k are Vosburg points.

ument dated and undated Vosburg complex analogues in eastern New York.

Still other Late Archaic components can be isolated at the Ewing site in both strata III and IV. The first of these components is characterized by small (or narrow) stemmed and side notched projectile points, some of which appear analogous to the Sylvan stemmed and

Sylvan side notched types of the Sylvan Lake complex in the Hudson Valley (Fig. 18), ca. 2500–1900 B.C. (Funk, 1976:247–254). Although found in association with extensive faunal remains in several fire-cracked rock features at the Ewing site, these point forms are even better represented at VT-CH-175 immediately adjoining the main locus of Ewing site (Cowan, 1977:5). Small numbers of Normanskill points (Fig. 18h–i) occur at the Ewing site and are seemingly indicative of a River phase component, ca. 1900–1500 B.C., as best known at the Bent and Pickle Hill sites, again in the Hudson Valley (Ritchie, 1965:125–132; Ritchie and Funk, 1973:52–70).

The final representation of the Late Archaic period at the Ewing site seems most clearly related to the Snook Kill or Batten Kill phases, ca. 1700–1400 B.C., although evidence of this component is scarce (Fig. 18d). Better understood representations of these phases have been investigated at the Snook Kill and the Kuhr sites in the Hudson and Susquehanna River drainages, respectively (Funk, 1976:259–263; Ritchie, 1958:91–98; Ritchie and Funk, 1973:49).

A hiatus in the record of utilization and occupation seems apparent at the Ewing site following the most recent Archaic component after ca. 1400 B.C. On the basis of ceramics, brief usage of Ewing and the adjoining VT-CH-175 occurred during the Middle Woodland period, particularly at the time of the Burnt Hill phase in New York (Funk, 1976:296–297), or as it is better known in local contexts, the Intervale phase, dated from A.D. 600 to A.D. 800 at the Winooski site (Fig. 19e, f) (Petersen, 1980:42–44; Petersen and Power, 1983:398–403). Recently obtained radiocarbon dates from the Ewing site corroborate such an Intervale phase occupation at A.D. 700 ± 270 on faunal remains from a small fire-cracked rock concentration and document the apparent presence of an Early Woodland occupation at 765 ± 135 B.C. from the remains of a dog eaten by the site's inhabitants (see Table 2).

The most recent component(s) at the Ewing site are attributable to the newly defined Shelburne phase, ca. A.D. 1000–A.D. 1700, which spans the entire Late Woodland period and the earliest Contact period. This phase represents the most intensive period of aboriginal usage of the pond. At Ewing confined largely to stratum IV, this occupation produced over a dozen hearth, fire-cracked rock concentration and post mold features. Diverse artifacts attributable to the Shelburne phase component(s) include diagnostic Levanna projectile points (Fig. 20), numerous ceramics (Figs. 19a–d, 21–22), bone, antler and tooth tools (Fig. 23), a mortar (Fig. 24), numerous other lithic tools and a wide array of subsistence remains. The diagnostic artifacts, particularly the ceramics, reveal similarities to the Owasco, proto-Iroquoian and possibly Contact period developments in New York, Ontario, and Quebec (for example, Ritchie, 1965:272–324; Ritchie and Funk, 1973:165–

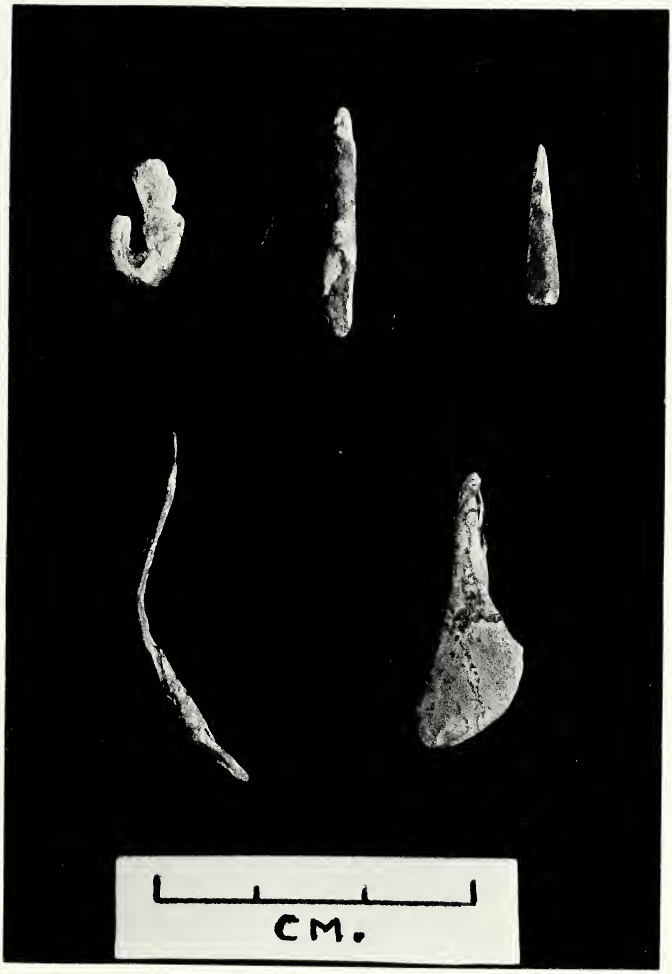

Fig. 15.—Late Archaic period (?) native copper artifacts from the Ewing site.

178; Clermont et al., 1983; Pendergast, 1966; Wright, 1966, 1979:62–75). Other more distant similarities can also be noted with complexes across the broader Northeast (for example, Bourque and Cox, 1981; Petersen, n.d.; Wright, 1979:74–91). We cannot, as of yet, make precise regional correlations and it seems likely that the Shelburne phase will ultimately prove to be distinctive in regional contexts (Ritchie, 1970: 21).

Although no European trade goods can be related to the Shelburne

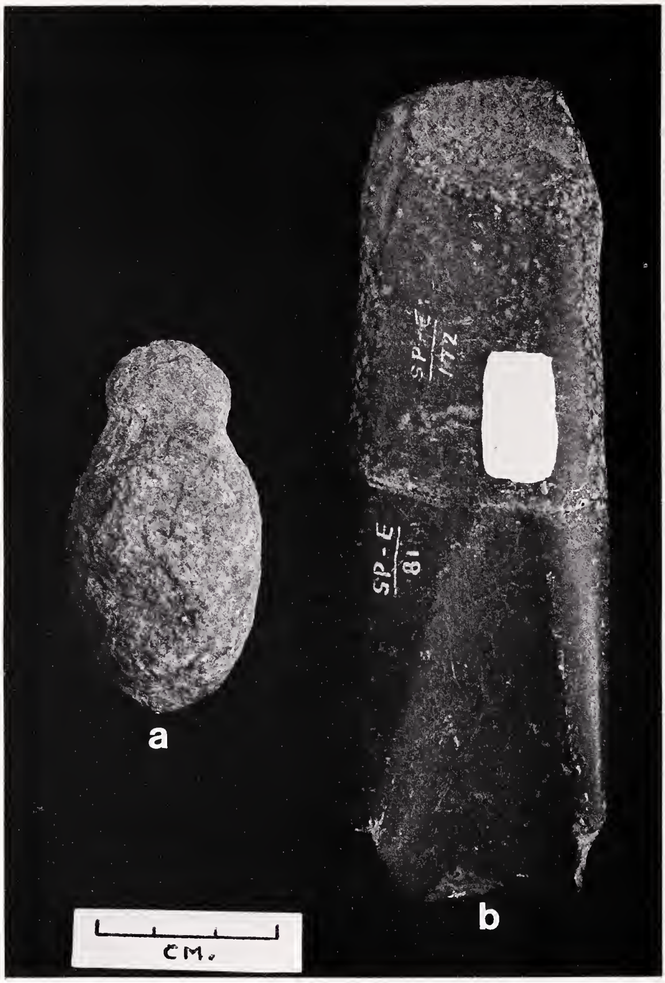

Fig. 16.—Late Archaic period groundstone artifacts from the Ewing site: a is a plummet; b is a gouge.

phase as of yet, it is clear that this phase persisted well into the Contact period on the basis of two dates on UVM feature 4 and closely related UVM feature 6 from the Ewing site. Here we have evidence for the late survival of native technologies in the late 17th century and possibly well into the 18th century (see Thomas, 1973, 1979).

Several contemporaneous sites have been recently identified in the Lake Champlain drainage. VT-FR-134, which is located on the flood-

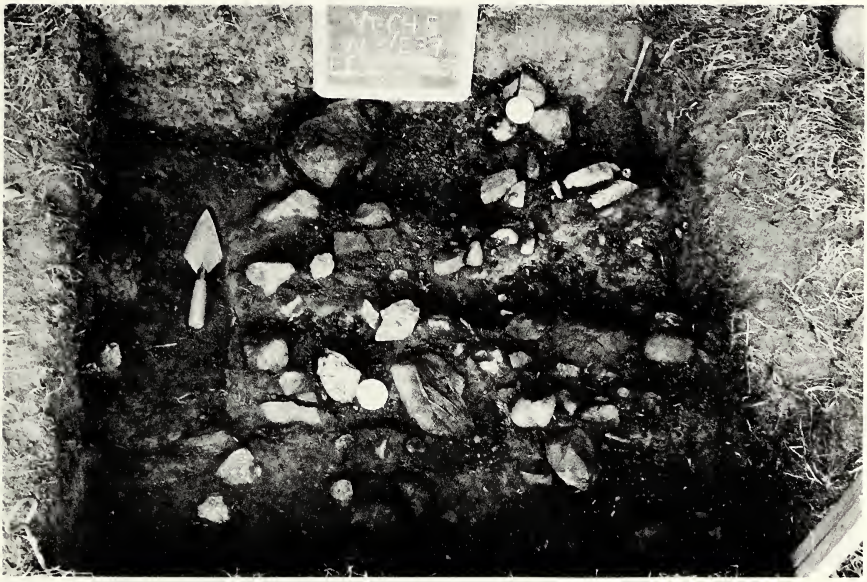

Fig. 17.—Late Archaic Ewing phase feature 5 fire-cracked rock concentration in stratum III in unit N3,4/E37,38 at the Ewing site facing north.

plain of the Missisquoi River, has produced a similar artifact inventory, but different feature types than present at the Ewing site; the same can be said of the Donohue site (VT-CH-94) on the floodplain of the Winooski River Intervale. The Donohue site is particularly important because it has provided unique evidence (to date) of mixed hunting and gathering and small scale cultivation of corn during the Late Woodland period. The Late Woodland occupation at VT-FR-134 has been dated to A.D. 1440 ± 90 and at the Donohue site to A.D. 1440 ± 125 and A.D. 1700 ± 115 (Bumstead, 1980; Peter A. Thomas, personal communication, January 1984).

A general consideration of all archaeological sites in the Shelburne Pond locality allows clarification and amplification of the sequence known from the Ewing site and provides evidence of most, if not all, known periods and subperiods of northeastern prehistory (see Table 5). The Auclair Site (VT-CH-3), with a large inventory of artifacts from primarily disturbed contexts, provides evidence of nearly continuous usage from at least the Early Archaic period onward. One possible Paleo-Indian projectile point basal fragment is known (Ritchie, 1970: Appendix, and personal examination), which suggests tentative usage of the Auclair site before ca. 9000–10,000 B.P. (7000–8000 B.C.) (see

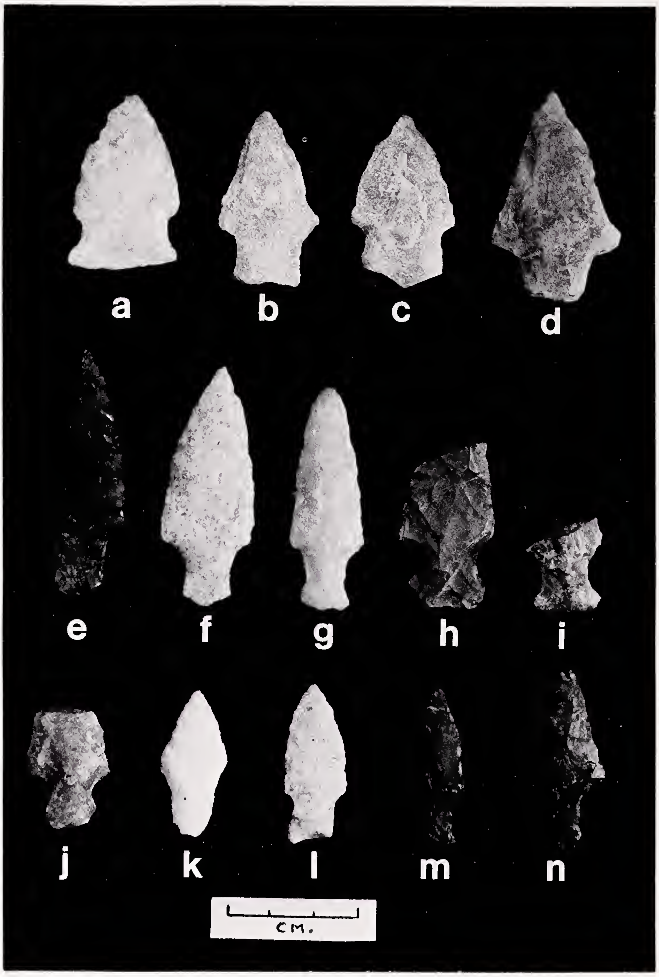

Fig. 18.—Late Archaic period projectile points from the Ewing site: a, c are Sylvan side notched-like points; d is a Snook Kill point; b, e, f, j–n are various stemmed points; g–i are Normanskill points.

Gramly, 1982; Loring, 1980; Ritchie, 1953, 1957). The Early Archaic period is more clearly represented at the Auclair (VT-CH-3) and Auclair II (VT-CH-8) sites, with both classic bifurcate base and Swanton corner notched points present (Fig. 25a–b). As mentioned for Swanton corner notched points in the discussion of the Ewing site, these forms are generally attributable to ca. 6500–5500 B.C. (for example, Broyles,

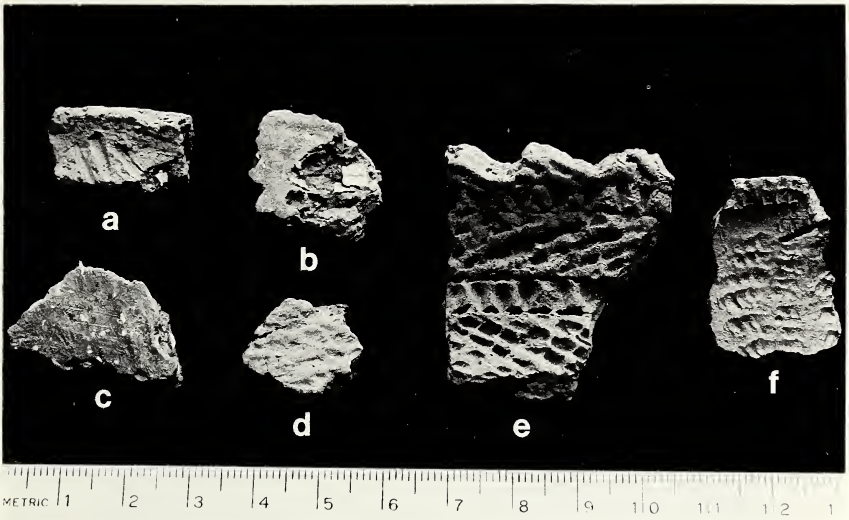

Fig. 19.—Middle Woodland and Late Woodland period ceramics from the Ewing site: a–d are Late Woodland shell-tempered sherds with the rim sherd (a) showing incised decoration; e, f are late Middle Woodland Intervale (Burnt Hill) phase rim sherds with dentate decoration. Specimen a is 23 mm long.

1971; Funk, 1979; Ritchie and Funk, 1973:38–29; Thomas and Robinson, 1983), although even later, more problematical associations are known (for example, Snow, 1977, 1980:169–170).

Middle Archaic period projectile points, including Neville and Stark types (Fig. 25c–e), are also present at the Auclair site. These are dated from 5500 B.C. to as late as 4000 B.C. (for example, Dincauze, 1976: 119–124; Funk, 1979:30; Starbuck, 1982).

Late Archaic period components are particularly well represented at the Auclair site, with a Vergennes phase component, ca. 3500–3000 B.C., evidenced by Otter Creek points and ground slate forms (Fig. 25f–h). Other Vergennes phase components are represented at VT-CH-2, VT-CH-25, VT-CH-110 and VT-CH-114, and as mentioned previously, at the Ewing site. Still later Late Archaic components in the Shelburne Pond locality include Ewing (Vosburg) phase components, ca. 3000–2500 B.C. at Auclair, VT-CH-6 and VT-CH-8, and small (narrow) stemmed point components, ca. 2500–1900 B.C., at Auclair, VT-CH-6, VT-CH-7, VT-CH-8 and VT-CH-134 (Fig. 25i).

Snook Kill or Batten Kill phase components, characterized by broad stemmed Susquehanna, Genessee, and Perkiomen points (Fig. 25j, k), are known from Auclair and VT-CH-2. These components can be

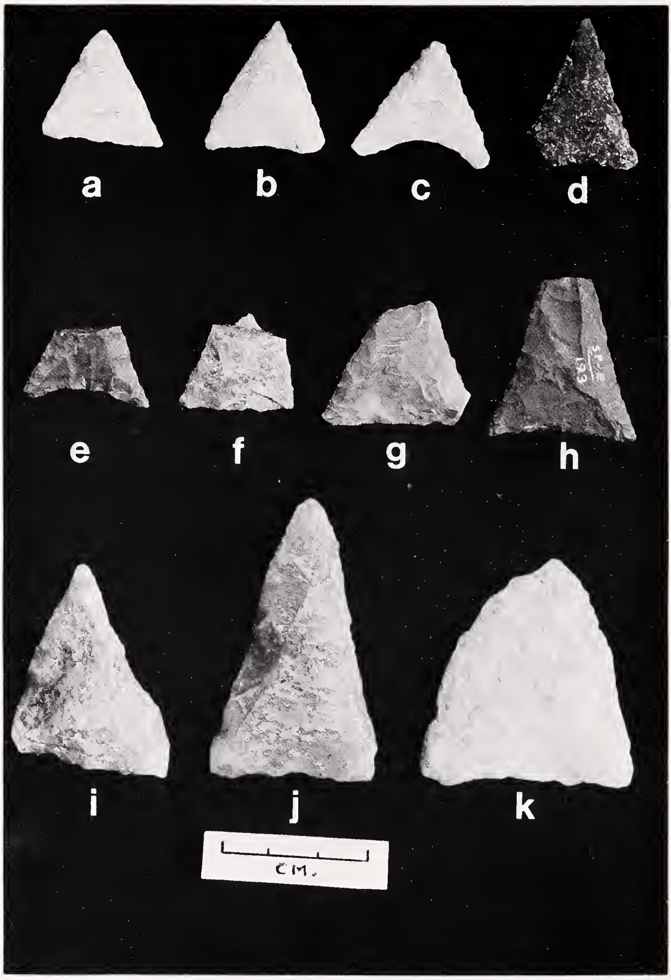

Fig. 20.—Late Woodland period projectile points and bifaces from the Ewing site; a–h are Levanna points; i–k are bifaces or biface preforms.

generally related to the Susquehanna or Broadspear tradition in eastern and southern New England (and elsewhere) and should date from ca. 1700–1400 B.C. (Borstel, 1982:64–65; Dincauze, 1976:113–114; Kenyon, 1980; Ritchie, 1969:219–223; Turnbaugh, 1975). The slightly later Orient phase is represented at Auclair and VT-CH-6 by Orient projectile points as well as steatite (soapstone) vessel fragments at Auclair (Fig. 26). The Orient phase has been dated between ca. 1100 B.C. and

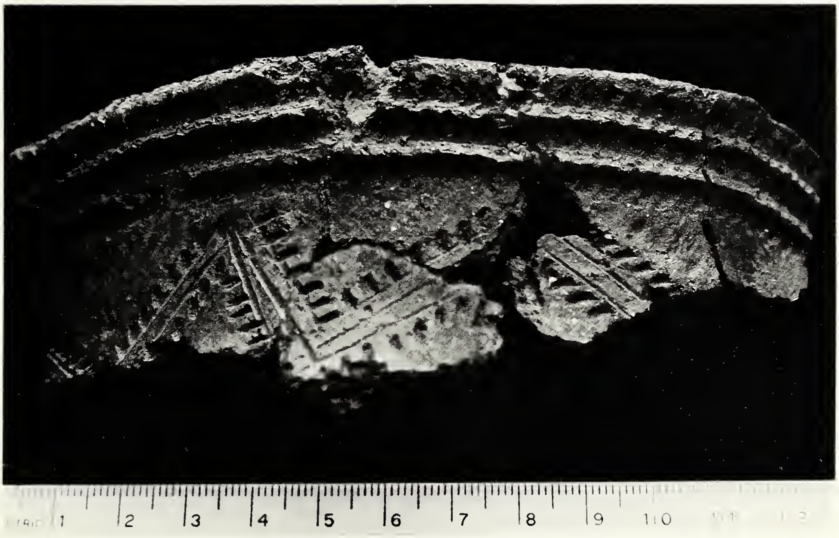

Fig. 21.—Late Woodland period ceramic rim sherd (with cord-wrapped stick, incised and punctate decoration) from the Ewing site. This vessel resembles the Castle Creek incised type. Specimen is 124 mm long.

750 B.C. in eastern New York (Ritchie, 1965:164–178; Funk and Lord, 1972:39) and to 800 B.C. ± 80 at the Sumner Falls site in the Connecticut River drainage of Vermont (Sargent, 1960, 1969).

One or more Early Woodland period components, ca. 1000 B.C.–100 B.C., are also represented in the Shelburne Pond locality based on diagnostic projectile points. Lobate base "Adena" points and classic Meadowood points are known from the Auclair site and VT-CH-6 (Fig. 25l, m). These may reflect contemporaneous relationships with Early Woodland mortuary sites known in the Lake Champlain drainage (see Haviland and Power, 1981:115–132), including the Boucher site (Basa, 1975) and several other sites, but the matter is still poorly understood. Parenthetically, the earliest widespread aboriginal ceramics in the Northeast, generally known by the type designation Vinette 1 (Doyle et al., 1982; Petersen and Hamilton, 1984), are not currently known from any of the Shelburne Pond sites.

Middle Woodland period components, ca. 100 B.C.–A.D. 1000, are also present in the Shelburne Pond locality. These include an early Middle Woodland Winooski phase component at VT-CH-175 (Ewing 5A), ca. 100 B.C.–A.D. 300 and an Intervale (Burnt Hill) phase component at the Ewing site and possibly, VT-CH-2 and VT-CH-226, ca.

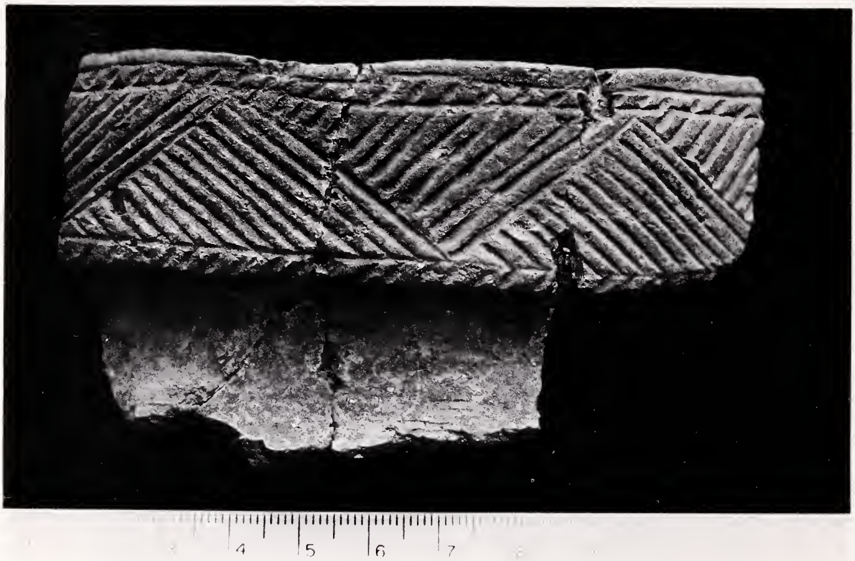

Fig. 22.—Late Woodland period ceramic rim sherd (with incised decoration) from the Ewing site. This vessel resembles the Durfee Underlined type. Specimen is 100 mm long.

A.D. 600–800, as noted above (Petersen, 1980; Petersen and Power, 1983:396–397, 398–403). A component possibly related to the Fox Creek phase, ca. A.D. 350–500 as defined in eastern New York (Funk, 1976:287–293), is represented at the Auclair site (see also Clermont and Chapdelaine, 1982:83; Ritchie, 1969:107–111; Ritchie and Funk, 1973:120–153). Terminal Middle Woodland Colchester phase ceramics are clearly present at the VT-CH-106 island site and likely at the Ewing site as well. The Colchester phase has been dated between A.D. 800 and A.D. 1050 at the Winooski site and VT-CH-146 in the Winooski River Intervale (Petersen, 1980; Petersen and Power, 1983: 403–406; see also Ritchie, 1965:205–266; Ritchie and Funk, 1973: 117–122).

With the onset of the Late Woodland period after ca. A.D. 1000, aboriginal utilization and occupation of the Shelburne Pond locality increased rather dramatically, following a trend apparently established in the Middle Woodland period (see Table 5). This increased usage is particularly evident in the Shelburne phase component(s) at the Ewing site, as noted above, but is also evidenced at a variety of other sites. These include VT-CH-2, VT-CH-3, VT-CH-4, VT-CH-6, VT-CH-8, VT-CH-25, VT-CH-110, VT-CH-131, VT-CH-133, VT-CH-175 (Ew-

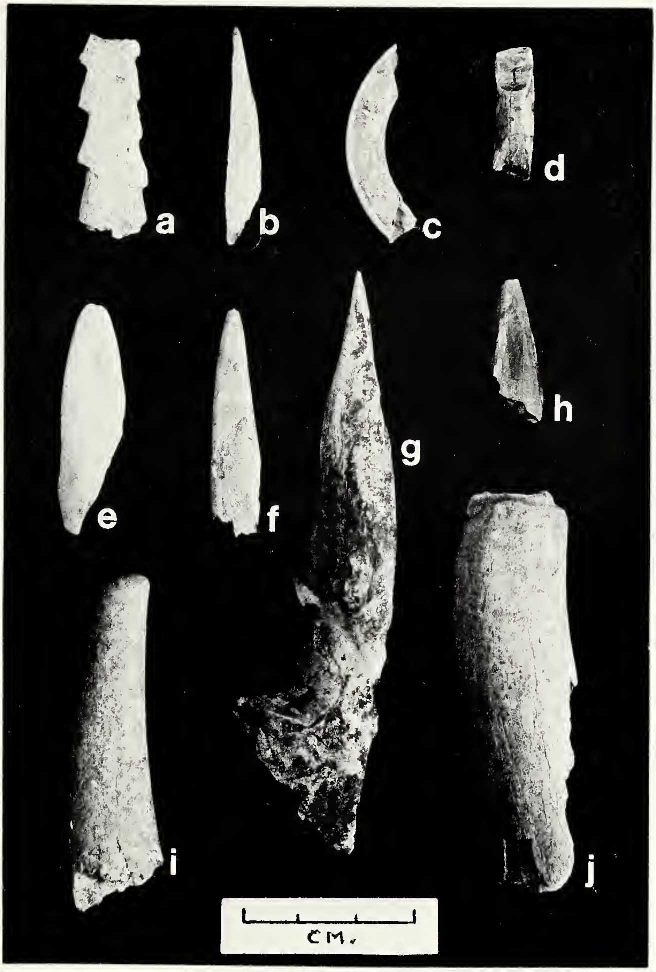

Fig. 23.—Bone, antler and tooth tools from the Ewing site: c, worked beaver incisor, and i, broken antler tine pressure flaker, are attributable to the Late Archaic period. All other specimens are attributable to the Late Woodland/Contact period (a, g, h, j) or lack provenience information (b, d–f).

ing 5A), VT-CH-224, VT-CH-226, VT-CH-227, and possibly VT-CH-106. A variety of Late Woodland components are also known from other localities in the Lake Champlain drainage, including the previously mentioned Donohue (VT-CH-94) and VT-FR-134 sites among

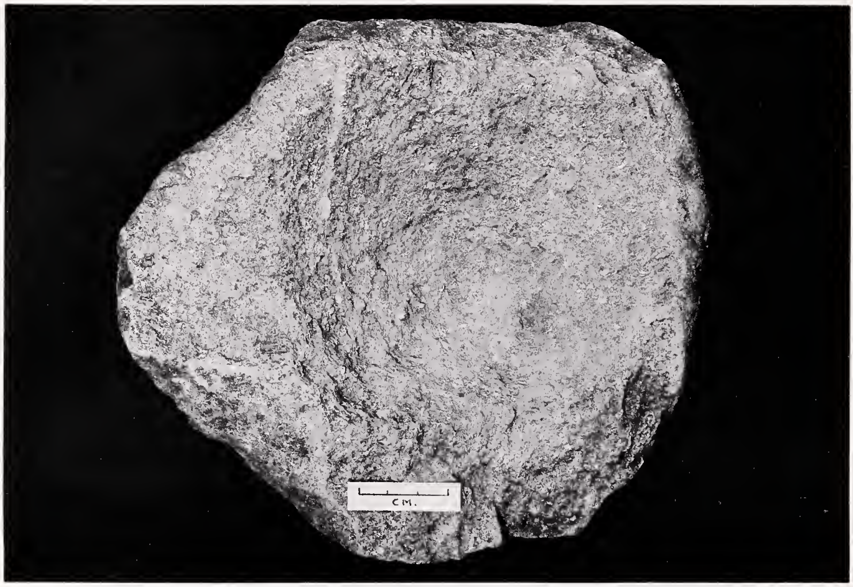

Fig. 24.—Late Woodland period mortar from the Ewing site.

others (see Bailey, 1937, 1939*a,* 1939*b,* 1940; Bumstead, 1980; Haviland and Power, 1981:132–147).

Evidence of protohistoric or Contact period aboriginal components can be documented only on the basis of radiocarbon dates from the Ewing site, with the latest evidence of utilization at about A.D. 1700. Protohistoric or Contact period artifacts have been also alluded to in earlier research (Hatch, 1943) on the pond, as noted above. Such evidence is definitely known from the local area, throughout New England and in adjoining Quebec as the latest recognizable evidence of native populations in the archaeological record (for example, Pendergast and Trigger, 1972; Petersen, n.d., Thomas, 1973, 1979).

SETTLEMENT AND SUBSISTENCE

This provisional outline should be considered more as a series of hypotheses about aboriginal utilization of the Shelburne Pond locality than as a firmly committed series of propositions. We hope to be able to explicate details of settlement and subsistence in our final report and thus be able to assess the details of hunter-gatherer adapatations in this confined setting. Unfortunately, the "grain size," or degree of resolution of the archaeological record is generally coarse (Binford, 1980:17; Thomas, 1983*b*:438–439) and this is certainly the case around

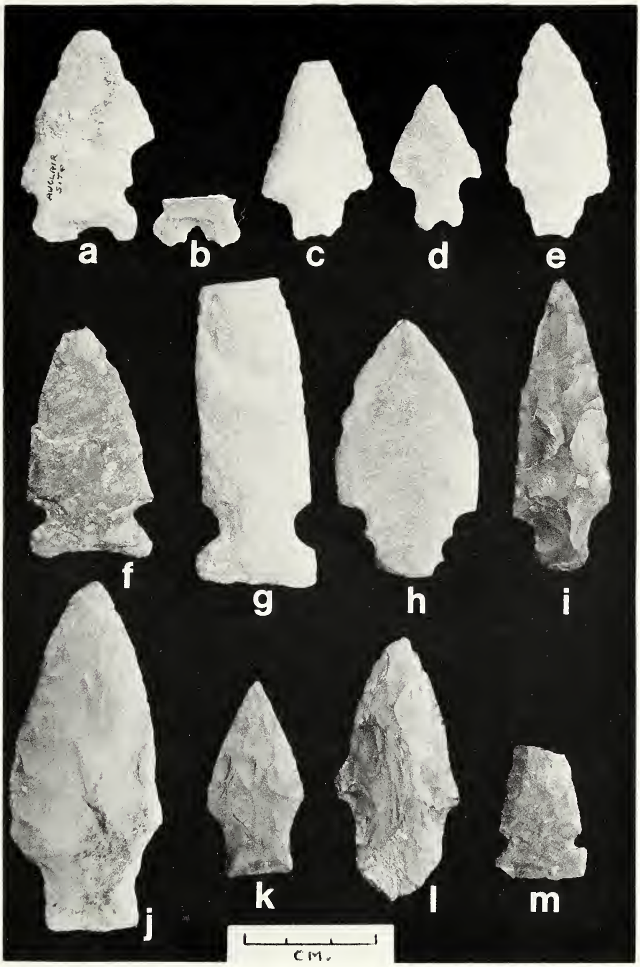

Fig. 25.—Early Archaic, Middle Archaic, Late Archaic and Early Woodland period projectile points from the Auclair I (VT-CH-3) site: a, b are bifurcate base points; c–e are Neville points; f, g are Otter Creek points; h is a ground slate point; i is a Poplar Island-like point; j, k are Susquehanna points; l is an Adena point; and m is a Meadowood point.

Shelburne Pond. The available sample will not provide fine-grained details with any degree of confidence at this point. Caution is therefore to be exercised in acceptance of the following hypotheses.

The currently available information on site size, content, and settings indicates that at least some of the locations were actual habitation sites,

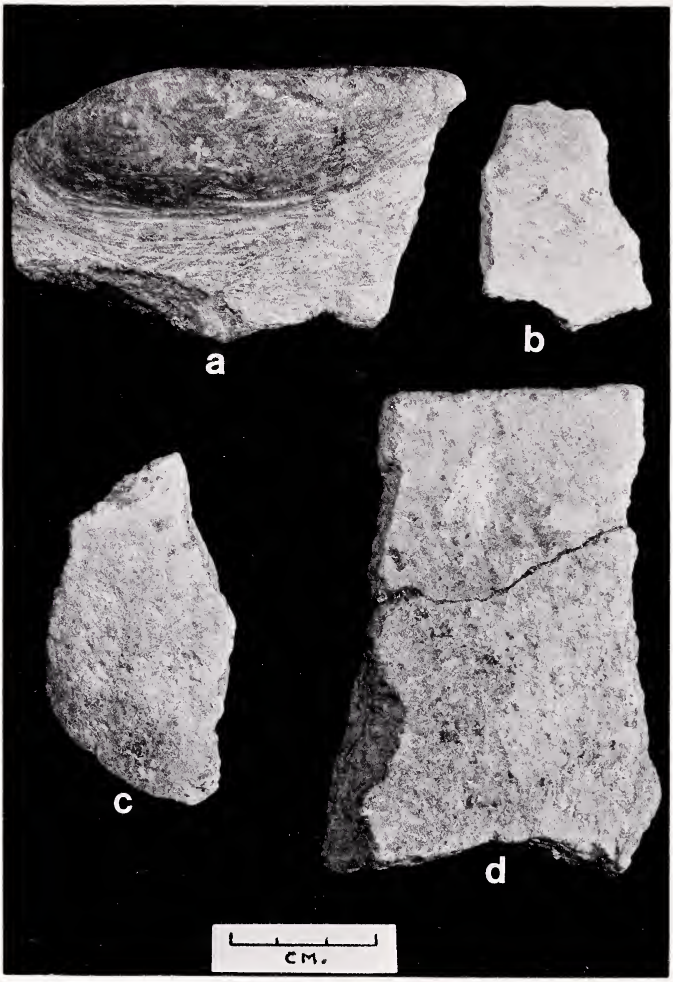

Fig. 26.—Late Archaic period steatite vessel fragments from the Auclair I site (VT-CH-3): a, d are rim sherds and b, c are body sherds. Note the lug handle on rim sherd a.

short term or seasonal camps, including sites such as Ewing, Auclair, VT-CH-2, and VT-CH-6. Other sites were more probably special purpose sites, utilized for fish, bird, or mammal exploitation and/or processing and the like. Special purpose utilization seems to be exemplified at sites such as VT-CH-25, VT-CH-169, VT-CH-228 and especially VT-CH-106 which is situated on a small bedrock island. The likelihood of different types of seasonal utilization at any one site over time must be carefully examined (see Binford, 1982:8–16). Thus, understanding of the settlement system of various users and inhabitants of the Shelburne Pond locality remains relatively imprecise, both within the local drainage and geographically continguous areas. It is also very likely that usage of the pond was integrated within a much broader pattern of seasonal movement within the Lake Champlain drainage.

Reconstruction of aboriginal subsistence, an important determinant of usage of the Shelburne Pond locality, is likewise limited by the restricted nature of the sample. Only two sites have produced subsistence remains (Ewing and VT-CH-106); of these, only one (Ewing) will permit internal temporal differentiation of a general sort. Tentative results derived from preliminary examination of the large sample from the Ewing site reveal a wide array of animal foods in the Late Woodland/Contact period Shelburne phase (Catania, 1978; Cowan, 1977:3; Haviland and Power, 1981:139; Arthur E. Spiess, personal communication, July 1983). The Late Woodland/Contact fauna includes immature and mature white-tailed deer (*Odocoileus virginianus*), elk or wapiti (*Cervus elaphus*), bear (*Ursus americanus*), dog (*Canis familiaris*), beaver (*Castor canadensis*), and muskrat (*Ondata zibethecus*) among other species of mammals. In addition, fish scales and other diagnostic faunal and floral remains document Shelburne phase usage of bullhead (*Ictalurus* sp.) and possibly perch, northern pike, and bass, as well as snapping turtle (*Cheydra s. serpentina*), unidentified birds, molluscs, hickory nuts (*Carya* sp.), butternuts (*Juglans cinerea*), and *Chenopodium* seeds.

Deer, bear, turtle, and fish are attributable to several of the Late Archaic features, including those from both the Ewing (Vosburg) and small stemmed components. Likewise, small mammal, large mammal, varying sized fish and turtle remains are attributable to Middle Woodland usage of VT-CH-106. It should be emphasized that these remains have yet to be subjected to systematic analysis as exemplified in treatments by Spiess (1978) and Spiess and Hedden (1983).

Data derived from the varied subsistence remains should enable us to roughly assess the constancy in utilization of local food resources in the Shelburne Pond locality over some or all of the known 8000 year span of usage. In particular, correlation of the aboriginal subsistence pattern(s) with the transition from biotic conditions of the open oligotrophic environment of Shelburne "Lake" before 1600 B.P. (A.D. 350) to the more eutrophic conditions of Shelburne Pond thereafter will be assessed. This transition and apparent increase in aquatic productivity may, in fact, help us "explain" the greatly increased usage of the locality in the Middle and Late Woodland/Contact periods. Increased usage of the more concentrated resources there after A.D. 350 certainly would have been a logical subsistence activity, particularly when seen in conjunction with relatively clear evidence of local population growth during the Middle Woodland period (Haviland and Power, 1981:107; Petersen and Power, 1983:387–406).

On the basis of these preliminary observations, as well as our knowledge of local soil and topographic conditions, we hypothesize that horticulture was never (or rarely) undertaken within the confines of the Shelburne Pond locality. Horticulture did not appear in the Lake Champlain drainge until well after A.D. 1000 and apparently did not provide a focus of aboriginal subsistence until after A.D. 1450 when it first appears in the local record. Historic documentation indicates the presence of extensive cultivated fields in the lower stretches of the major tributaries of Lake Champlain by the 17th Century (A.D. 1609) when Samuel de Champlain made the first recorded visit to the valley (Bourne, 1906:207). The fragmentary ethnographic record of aboriginal subsistence for the local Western Abenaki inhabitants (Day, 1971, 1978; Haviland and Power, 1981:151–164; Thomas, 1973, 1979) provides additional details of the obviously mixed diet of cultivated corn, beans, and other crops with the more traditional native resources used by long term local hunter-gatherers. Seasonal mobility was characteristic of Western Abenaki populations of the Lake Champlain and adjoining drainages, ranging from aggregated villages near cultivated fields to seasonal small family and task group sorties in the mid-autumn to mid-winter and mid-summer seasons.

A recent study of fiber perishables (basketry, cordage, and other materials) reconstructed from the Ewing site and others in northern New England documents a notable difference in diagnostic attributes between Ewing site samples, other presumably proto-Western Abenaki and known Western Abenaki samples (Petersen and Hamilton [with LaBar and Hedden], 1984). Thus, we plan to investigate further the possibly intrusive nature of the Late Woodland/Contact period inhabitants of the Shelburne Pond locality, a matter beyond the scope of the present paper.

Regardless of whether or not any or all of the aboriginal populations utilizing the Shelburne Pond locality were proto-Western Abenaki or Western Abenaki, it seems evident that the primary, if not sole focus of such utilization was the diverse natural resources to be found there. The generally small site sizes, the apparently limited nature of material inventories at most sites, and the particular nature of site content and character (for example, extensive fire-cracked rock concentrations) all suggest a very different pattern of utilization than at other well known archaeological sites and site districts within the Lake Champlain drainage. For example, one composite feature (see Fig. 12) in the recent UVM reinvestigation at the Ewing site produced more than twice as large a volume of fire-cracked rocks (5300 [+] specimens weighing over

318 kg) than the entire excavation at sites twenty times more extensively excavated, such as at the Winooski site, VT-CH-146, and VT-FR-134. We may safely attribute these concentrations at Ewing and other sites in the Shelburne Pond locality to patterns of different cumulative activity between Shelburne Pond and the floodplain sites mentioned here.

It is also possible, if not likely, that this differentiation of activity between the Shelburne Pond locality and riverine (or lacustrine) settings was more firmly established in the Woodland period, when larger social aggregates were seasonally present in lowland settings near Lake Champlain. Earlier Archaic period (and Paleo-Indian) components seem to have been smaller in scale and less well differentiated between sites, while not being uniform across all site situations and environments. In this model, throughout its chronological span, the Shelburne Pond locality would have served as the scene of activities characteristic of small hunter-gatherer camps and special use areas, with more special-purpose utilization (for example, fish or large mammal procurement and processing) likely during the Woodland period, particularly the Late Woodland/Contact period after A.D. 1000. Further research and hypothesis testing are needed to better establish this and the other tentative suggestions offered here.

OVERVIEW

The record of archaeological variation in the Shelburne Pond locality is of great significance. Documentation of 8000 (+) years of nearly continuous usage by aboriginal peoples at 31 sites allows us to sense, if not fully understand, the proficiency of hunter-gatherer adaptations in a temperate forest setting. These people most likely did not use, or live at, Shelburne Pond year round any time within the span of its history. They did return again and again to use the localized riches of the pond environments however, and in this we begin to have a sense of the cycles which characterize hunter-gatherer activities in "optimal" environments. That their lives should be reduced to a discussion of economics is a travesty of sorts, especially since their social-ceremonial world was probably especially rich. We are forced to focus on economics and technology by the nature of the archaeological record.

The study of faunal remains indicates that food resources were rich and varied in and around Shelburne Pond, and that this condition was even more likely the case after A.D. 350 when the modern pond with its marshes was "born." As students of human ecology, we take this to be an exciting and potentially promising correlation, worthy of further study and testing. Moreover, the apparent differentiation of site usage between the Shelburne Pond locality and sites in nearby local riverine settings at once helps us to better fathom the patterns of human mobility, its seasonal nature and the scale and range of such movement, matters little understood and frequently overlooked in the context of contemporary sedentism. These and a host of other questions remain the challenge and attraction of archaeological research in general.

ACKNOWLEDGMENTS

A large number of individuals and organizations have contributed to the success of this research, past and present. First, we would like to acknowledge the Cecil Howard Charitable Trust, the Vermont Historical Society, and the Vermont Division for Historic Preservation for their critical financial support, which made it possible for us to look at all archaeological sites in the Shelburne Pond locality and thus develop a synthetic perspective. In particular, Giovanna Peebles, State Archaeologist for the Division for Historic Preservation, provided considerable support in terms of the site survey and radiocarbon dating. Dr. Ian Worley and the UVM Environmental Program provided critical access to the H. Laurence Achilles Natural Area, as well as several radiocarbon dates and background paleoenvironmental data. The University of Vermont Department of Anthropology also played an important role in the development of our understanding of the study area through inviting Petersen to teach the summer field school in archaeology. Petersen would like to especially acknowledge the continued support of Dr. Marjory Power and Dr. William Haviland, friends and counselors over the years, Dr. Peter Thomas for his patient advice, and Dr. Peter Woolfson, Department Chair, who, in a like manner, used his patience to insure smooth administration of many organizational details. Of equal importance, various members of the Vermont Archaeological Society, in particular, William Noel, past President of that organization, and Dee Brightstar, current President, were instrumental in providing access to research collections and have provided general support over the course of the project, along with a host of VAS volunteer excavators and lab workers who will be mentioned in the final report.

Nathan D. Hamilton and Jack A. Wolford, then both graduate students in the Department of Anthropology at the University of Pittsburgh, conducted the 1983 Shelburne Pond intensive site survey. Laureen A. LaBar, a senior student in the Department of Anthropology at the University of Vermont, served as teaching assistant for the 1983 UVM field school.

Other supporters of the 1983 field research include Zita and Sawyer Lee, who provided critical access across their property and as a result had to bear with daily, dusty traffic and often boisterous archaeologists. Ken Varney and Louise Basa were very generous in their own ways, both interested enough in our work on Shelburne Pond to make frequent visits and to provide all they could in the way of past information and material. Peter Beblowski provided important background and field geological data with his usual generosity and Charles Paquin not only helped with background logistics, but also often provided a welcome dinner for staff and crew. Sarah Burke is thanked especially for managing nearly all of the data entry over a long period, as is Michael Heckenberger for meritorious service, particularly in "wrestling" with the voluminous fire-cracked rocks. Of course, all of the 20 1983 field school students should be thanked for their diligent work at the Ewing site, often under trying conditions. These individuals include: Nancy Barthold, Robert Bartone, Katy Blackmer, Sarah Burke, Jean-Marc Chemla, Sheila Crowley, David DuBrul, Louise DuBrul, Peter Ewing, Michael Heckenberger, Andrea Horan, Constance Keedle, Edward Knight, Marlene Levine, Tara Prindle, Martha Roberts, Laura Stepanski, Suzanne Stritzler, Kelly Thompson and Tamsen Vandermeer. The 25 volunteer excavators, too numerous to mention in this initial report are likewise thanked. It seems likely that we all will long remember the spectacular days spent on Shelburne Pond, the occasional clear blue days of July and the rains sweeping across the pond in August.

Our reviewers included Dr. Arthur Spiess of the Maine Historic Preservation Commission, Dr. William Haviland and Giovanna Peebles. We have given serious consideration to all of their comments, but have had to follow our own inclinations in some instances here. Finally, Petersen would like to once again thank Frank Cowan for providing his first introduction to archaeological field work at the Ewing site and for sharing thoughts about the potential of Shelburne Pond research some years past. As is customary, we accept full responsibility for any errors or omissions in this report.

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PALEO-ARCHAEOLOGICAL AND HISTORICAL RECORDS OF SELECTED PENNSYLVANIA MAMMALS

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Abstract

Historical, archaeological, and paleontological records, as well as specimen records from research collections, were compiled to gain a better understanding of the relative abundance and distribution of selected Pennsylvania mammals. Those species selected are considered extirpated, rare, or worthy of special comment. Species discussed include *Castor canadensis, Canis latrans, Canis lupus, Gulo gulo, Martes americana, Martes pennanti, Taxidea taxus, Felis concolor, Lynx canadensis, Lynx rufus, Alces alces, Cervus elaphus, Odocoileus virginianus, Rangifer tarandus,* and *Bison bison.* Accounts include a tabulation and map of the available records.

Introduction

The intentional or inadvertent activities of man have caused many species to become extirpated or rare over large geographical regions of the continent. The Commonwealth of Pennsylvania and adjacent areas represent one of these areas for several species of Recent mammals.

Rhoads (1903) reported the beaver (*Castor canadensis*), wolf (*Canis lupus*), cougar (*Felix concolor*), wapiti (*Cervus elaphus*), and bison (*Bison bison*) to be extinct in Pennsylvania. Shoemaker (1917, 1919) discussed the folklore and facts surrounding the extermination of these

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species as well as the wolverine (*Gulo gulo*), marten (*Martes americana*), fisher (*Martes pennanti*), Canadian lynx (*Lynx canadensis*), and moose (*Alces alces*). Some of the extirpated species were subsequently introduced (*Castor canadensis, Cervus elaphus,* and *Bison bison*); others (*Martes americana* and *Martes pennanti*) are possibly moving into Pennsylvania. However, in many cases these species are considered rare in the Commonwealth. There are a few species of Pennsylvania mammals that are worth mentioning because of their unusual history in the Commonwealth. These species include the coyote (*Canis latrans*), badger (*Taxidea taxus*), bobcat (*Lynx rufus*), white-tailed deer (*Odocoileus virginianus*), and caribou (*Rangifer tarandus*).

There are considerable historical data, as well as archaeological and paleontological information, concerning extirpated and rare Pennsylvania mammals. However, no attempts have been made previously to summarize these data in a cohesive report. The following is a review of this information to determine former distributions and relative abundance of selected extirpated and rare mammals from Pennsylvania. The species included in this study are *Castor canadensis, Canis lupus, Canis latrans, Gulo gulo, Martes americana, Martes pennanti, Taxidea taxus, Felis concolor, Lynx canadensis, Lynx rufus, Alces alces, Cervus elaphus, Odocoileus virginianus, Rangifer tarandus,* and *Bison bison.*

METHODS

To determine the former distribution and abundance of the species studied, various sources of information were consulted, including paleontological records, archaeological records, historical records, published Recent records from books and journals, and specimen records in research collections. Excerpts from newspaper articles and other historical records were made available by the Pennsylvania Game Commission. By going back to the original articles, over 95% of the Pennsylvania Game Commission reports used in this study were verified.

When reviewing these sources of information, specific types of information were collected. Generally, situations involving actual "contact" with the specimen were included in this study. A contact record is an account involving a killed or captured animal. Because the animal was "in hand," identification would be less questionable. All contact records were included even if the identification of the mammal was possibily erroneous. Because some questionable records had been perpetuated through time, it was necessary to include such records for further discussion. If contact records were rare, sightings, tracks, or related reports were included. Such non-contact reports also became significant as populations of various species declined. In general, efforts were made to utilize records which provided a date, locality, and a contact incident. This information was tabulated with the reference of each record. Finally, all these records were mapped to indicate the possible historical distribution of the species.

DISCUSSION

A review of sources of information resulted in several problems. One problem encountered was separating fact from folklore in the historical accounts. Many of the earlier accounts contained tales loosely based on facts. For instance, Shoemaker, one of our primary sources of pre-1900 records, often wove stories of romance and adventure into his factual accounts. This was evident in his book, *Extinct Pennsylvania Animals,* Part II (Shoemaker, 1919). In the introduction, Shoemaker wrote, "The folklore and the traditions clustering about them like a diadem of romance, in addition to the general historical outline of their extermination will be the principal aim of this present volume." Although Shoemaker provided one of the few sources of early records on Pennsylvania mammals, Guilday (1963) remarked that "Some of the material is no doubt authentic, but most of it is embellished folklore and hearsay uncritically presented." To further compound the problem of folklore, there was an obvious tendency for many stories to be perpetuated through time by numerous and often well-respected authors. For this study, records provided by early folklorists were included, knowing that they may represent tales instead of factual accounts; thus, the value placed on these accounts will be at the discretion of the reader.

Bounty records, a good indication of the historical distribution of mammals, also presented some problems. During the early days of the bounty system, the mammals presented for bounty were identified by magistrates, justices of the peace, county commissioners, and mail clerks, rather than by trained agents of the Commonwealth or federal government. Thus, some bounty identifications were dubious. Fraud also affected the reliability of bounty records. In the late 1800's, "pieces of wornout buffalo robes, mule hides, colt skins, etc." were used to imitate heads and ears of wild cats, wolves, and other species (Warren, 1897*a*). Exaggerated stories narrated by bounty hunters, and recorded for posterity also added to the confusion. Bounty hunters would brag about trapping or shooting large animals that were a threat to man but not about more innocuous carnivores like the marten and fisher. Finally, the number of bounty claims on a particular mammal was not necessarily a good indication of its relative abundance. According to bounty procedures, only one bounty affidavit was written up for every species of animal presented by the hunter regardless of the number of animals involved. Thus, a single bounty claim for wolves might represent one or more animals (Gerstell, 1936*b*).

The interpretation of common names for local fauna was a problem encountered throughout the literature. Killed and captured mammals were often identified by amateurs resulting in many mammals being misnamed. For instance, Poole (1932) commented that ". . . so few sportsmen and farmers have even the remotest idea of our native fauna. Many reports of 'wild cats' have been found on investigation to refer to house cats that have run wild and grown to enormous size." A very common nomenclatural problem also occurred when several species of mammals were given the same common name. For example, the mountain lion and bay lynx were both called wild cats. To further complicate the problem, one species might be given several common names. The bobcat was called the wild cat, bay lynx, catamount, mountain cat, tiger cat, and wolverine (DeKay, 1842; Rhoads, 1903; Seaton, 1929*d*; Warren, 1897*b*).

Recent kills or sightings of apparently extirpated mammals presented a fourth problem in this study. It was difficult to determine whether such animals represented escapees from roadside zoos or menageries, or whether they were truly wild members of the species. For example, the last cougar killed in Pennsylvania (1967) was probably an animal originating from Central or South American stock that had escaped from captivity (McGinnis, 1982).

Another problem involved misidentifications that were published in scientific journals and popular periodicals. Publication of identifications did not necessarily mean the identification was correct. Guilday (1963) pointed out that reported buffalo bones from archaeological sites may have been cow bones. Also, Pennsylvania Game News (Anon., 1934*b*; Harrison, 1948*b*) reported the killing of the last Pennsylvania gray wolf in 1907. This specimen was deposited at the Carnegie Museum of Natural History and was subsequently identified as a coyote (McGinnis, 1979).

Although archaeological records may document the presence of some species, the absence of other species does not reflect their occurrence. Research by N. A. Commeau (Guilday, 1961*b*) showed that as a sign of respect, certain northern Canadian Indian groups transported bones of slain animals from the areas where they were eaten to remote areas away from camp. Guilday (1961*b*) suggested that Pennsylvania groups may have had a similar ritual.

The plotting of locality records was difficult due to changes in county boundaries since Colonial time. In 1730, the Commonwealth of Pennsylvania consisted of four counties; by 1932 the number of counties was 67. For instance, a mammal caught in Lycoming County in 1800 might not be located in the same county using current county maps.

Finally, the reporting of historical records may be skewed by time and location with respect to settlement of various parts of the Commonwealth. There may have also been differential reporting based on local interpretations of the significance of a species.

There are many problems inherent to a study such as this, and it is important to keep these in mind. However, it is hoped that by indicating points of confusion, new sightings and contact records will be less nebulous and that interest can be stimulated for reporting information on these animals.

ACCOUNTS

Castor canadensis—beaver

Castor canadensis, commonly referred to as the beaver, was also called the castor or castor cat (Shoemaker, 1929). The beaver typically occurred with its primary food source, the aspen. Prior to man's influence, this area included all of the eastern United States except Florida and most of Georgia and North and South Carolina (Seton, 1929*e*; Warren, 1927). It was reported that the beaver was locally abundant in areas throughout Pennsylvania (Luttringer, 1931; Morgan, 1868). Rhoads (1903) reported that at one time populations of the beaver were numerous in mountain lakes and the headwaters of the Allegheny and Susquehanna rivers.

Remains of the beaver are quite common in paleontological and archaeological sites in Pennsylvania (Table 1). The oldest known paleo-archeological records are from Washington (11,300 B.P.) and Huntingdon (pre-4000 B.C.) counties (Guilday and Parmalee, 1965; Guilday and Tanner, 1962). Skeletal remains from archaeological sites have been recorded through historical times (Guilday, 1970). Early historic records date back to the 1700's. Pennypacker (1872) reported 24 individuals captured during 1730 and 1731. Approximately 100 years later, evidence of a population decline was apparent (Table 1; Fig. 1). One of the last records commonly reported for Clearfield County was an individual killed in 1837 (Anon., 1968*b*; Luttringer, 1931; Rhoads, 1903; Warren, 1897*a*). Although according to one source, no beaver records were reported from 1902 to 1915 (Anon., 1968*b*), Shoemaker (1919) reported one female killed in Union County in 1912. This constitutes the last account of the native beaver in Pennsylvania.

Extensive trapping and logging from colonial times up to the early twentieth century contributed to the extirpation of the beaver (Luttringer, 1931; Shoemaker, 1919). Based on historical records, Rhoads (1903) felt that beaver receded in a westerly direction. However, our records suggest a northeasterly direction (Fig. 1). Records showed that beaver were extirpated in the east in about 1830, from the headwaters of the west branch of the Susquehanna (Clinton County) in about 1840, and from Elk, Clarion, and Centre counties in about 1850–1865.

Rhoades (1903) commented on beaver recurring in Monroe County as a result of migrations of imported stock from New Jersey. In 1917, the beaver (probably *C. c. canadensis*) was introduced into Pennsylvania. The first pair came from Wisconsin and were released in Cowley Run in Cameron County. Within a few years, this pair developed into an established population in Cameron and southern McKean counties. Some of these individuals were moved to Clinton County. Between 1919 and 1922, 34 pairs were acquired from Canada and released at

Table 1.—*Paleo-archaeological and historical records of* Castor canadensis *from Pennsylvania.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
N.D.	Allegheny Co., O'Hara Twp., Blawnox Site (36A119)	Skeletal parts	Guilday et al., 1980
N.D.	Armstrong Co., East Franklin Twp., Walkchalk Rockshelter (36Ar15)	Skeletal parts	Guilday et al., 1980
N.D.	Armstrong Co., Mahoning Twp., Wadding Rockshelter (36Ar21)	Skeletal parts	George and Bassinger, 1975; Guilday et al., 1980
N.D.	Armstrong Co., South Buffalo Twp., Murphy's Old House Site (36Ar129)	Skeletal parts	Guilday et al., 1980
N.D.	Beaver Co., Hanover Twp., Buchanan Rockshelter (36Bv83)	1 skeletal part	Greene, 1961
N.D.	Fayette Co., Henry Clay Twp., 4 mi S Somerfield, Martin Site (36Fa23)	Skeletal parts	Gilmore, 1946
N.D.	Fayette Co., Springhill Twp., 3 mi S Monongahela R. and 1½ mi S George's Cr., Phillips Site (36Fa22)	Skeletal parts	Gilmore, 1946
N.D.	Greene Co., Cumberland Twp., Hartley Site (36Gr23)	Skeletal parts	Guilday et al., 1980
N.D.	Somerset Co., Addison Twp., 4 mi E Confluence, Fort Hill Site (36So2)	Skeletal parts	Gilmore, 1946
N.D.	Venango Co., Canal Twp., Venango Manor (36Ve18)	Skeletal parts	Guilday et al., 1980
N.D.	Venango Co., Scrubgrass Twp., Counterfeiters Cave (36Ve30)	Skeletal parts	Guilday et al., 1980
N.D.	Washington Co., North Strabane Twp., Boyle Site (36Wh19)	12 skeletal parts	Nale, 1963

Table 1.—*Continued.*

Date	Locality	Comments	References
	PALEO-ARCHEOLOGICAL RECORDS		
N.D.	Washington Co., Hanover Twp., Scarem Site (36Wh22)	15 skeletal parts representing 4 individuals	Mayer-Oakes, 1954
N.D.	Westmoreland Cc., (location of New Kensington) Racetrack Site (36Wm32)	Skeletal parts	Guilday et al., 1980
Pleistocene	Montgomery Co., on Schuylkill R., below Valley Forge, Port Kennedy Cave	1 specimen	Guilday, 1976
Quaternary	Monroe Co., 2½ mi SW Stroudsburg, Hartman Cave (=Crystal Hill Cave)	4 mandibular rami and other skeletal parts	Leidy, 1889
Recent	Cumberland Co., Carlisle caves	Skeletal parts	Miller, 1940
11,300 ± 700 BP	Washington Co., Jefferson Twp., Meadowcroft Rockshelter (36Wh297)	16 skeletal parts	Guilday et al., 1980
Pre-4000 BC	Huntingdon Co., W bank Raystown Branch of Juniata R., Sheep Rock Shelter (36Hu1)	27 skeletal parts representing 3 individuals	Guilday and Parmalee, 1965
100 BC–900 AD	Venango Co., Sandy Cr. Twp., 3 mi SE Franklin, Quaker State Rockshelter (36Ve27)	18 skeletal parts	Guilday and Tanner, 1962
1100 AD	Allegheny Co., Collier Twp., Drew Site (36A162)	4 skeletal parts representing 1 individual	Buker, 1970
1180 AD	Westmoreland Co., Penn Twp., Ryan Site (36Wm23)	4 skeletal parts	George, 1974
1190 AD	Somerset Co., Summit Twp., Gnagey Site (36So55)	125 skeletal parts	George, 1983
1200–1400 AD	Greene Co., 4½ mi S Waynesburg, Varner Site (36Gr1)	37 skeletal parts	Guilday, 1961
1330 AD	Allegheny Co., Stowe Twp., McKees	41 skeletal parts representing 7 individ-	Lang, 1968

Table 1.—*Continued.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
	Rocks Village Site (36Al16)	uals	
1390 ± 105 AD	Butler Co., Summit Twp., Bonnie Brook Site (36Bt43)	7 skeletal parts representing 2 individuals	Herbstritt, 1981
1400–1425 AD	Fayette Co., Redstone Twp., Campbell Site (36Fa26)	Skeletal parts	Guilday et al., 1980
1500–1600 AD	Indiana Co., Blairsville, Johnston Site (36In2)	11 skeletal parts	Guilday, 1955
1600–1625 AD	Lancaster Co., Washington Boro, 3 mi S Columbia, Eschelman Site (36La12)	226 skeletal parts representing 13 individuals	Guilday et al., 1962
1758–1766 AD	Westmoreland Co., Fort Ligonier (36Wm71)	2 individuals	Guilday, 1970
	HISTORICAL RECORDS		
1730–1731	Chester Co., near Phoenixville, on island in Schuylkill R.	24 caught by F. Buckwalter	Pennypacker, 1872
1748	Beaver Co.	7 skins presented by Wandots	Thwaites, 1904
1790	Cameron Co. near Grass Flat Islands near Sinnemahoning Cr.	1 caught by McLaughlin	Meginness, 1887
1818–1820	Sullivan Co., 4 mi above Lopez	2 caught by J. Robinson	Rhoads, 1903
1835	Venango Co. (western part)	1 trapped	Hazard, 1835
1837	Clearfield Co. (present site of Houtzdale)	1 killed; reported by A. Neveling to be last killed in county	Anon., 1968*b*; Luttringer, 1931; Rhoads, 1903; Warren, 1897*a*
1839	McKean Co., Beaver Meadow, approximately 2 mi above Kinzua Viaduct	2 or 3 caught by Jerod Robinson	Rhoads, 1903
1840	Clearfield Co., near Sabula	1 killed by W. Dixon	McKnight, 1905*a*
Pre-Civil War (1861)	Clinton Co., Kammerdiner Run (tributary of McElhattan Run)	2 killed by A. Staake	Shoemaker, 1919

Table 1.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1863	Clinton Co., Kammerdiner Run (tributary of McElhatten Run)	1 killed by J. Stake	Shoemaker, 1929
1864	Clarion Co., on Sandy Cr. near the Venango Co. line	1 killed; Zendle reported last killed on Sandy Cr.	Rhoads, 1903
Pre-1880	Wayne Co., Honesdale	1 killed; reported to be last killed (in county)	Rhoads, 1903
Pre-1880	Wayne Co., Salem Twp.	1 trapped by E. Nicholson	Rhoads, 1903
1884	Clinton Co., Pine Cr.	1 killed; reported by S. Nelson to be last killed on Pine Cr.	Anon., 1968*b*; Luttringer, 1931; Rhoads, 1903
1885	Snyder or Mifflin Co.	1 trapped on Swift Run; mounted specimen owned by Mr. Boak	Shoemaker, 1941
1885	Clinton Co., Shingle Branch of Young Woman's Cr.	1 killed by J. Stiles	Shoemaker, 1919
1899	Cambria Co., branch S. fork Little Conemaugh R.	1 observed by W. C. McHenry	Rhoads, 1903
1912	Union Co., Lick Run, (tributary of White Deer Cr.)	1 female killed by "the village idiot"	Shoemaker, 1919
	SPECIMEN RECORDS (Records prior to 1925)		
1922	Westmoreland Co., Rector	Killed 24 Nov, originated from imported stock (see text); skin preserved	WPMM M696; William Penn Memorial Museum
1922	Westmoreland Co., Rector	Killed 9 Dec by J. M. Phillips, obtained from imported stock (see text); skin, skull, and body skeleton preserved	CM 5319; Carnegie Museum of Natural History

game refuges throughout the Commonwealth (Luttringer, 1933). In 1924, 12 pairs were acquired from New York and released on game refuges. In 1931, it was estimated that over 4800 beaver inhabited Pennsylvania. Natural dispersal, assisted with stocking, has allowed

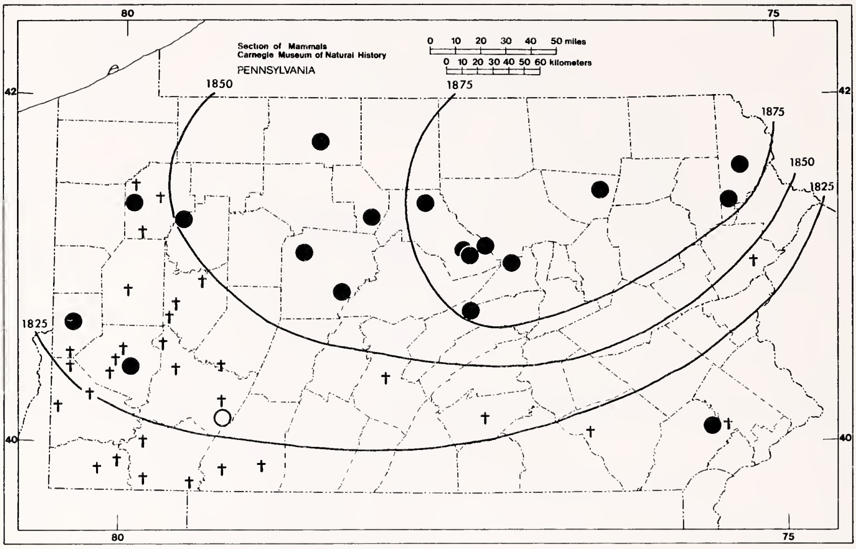

Fig. 1.—Map of Pennsylvania showing locations of records of *Castor canadensis.* Solid dots represent historical records of beaver captured or killed; open dots represent specimens in museum collections (half-open dots represent museum specimens that have written historical records associated with them); crosses represent records from paleontological or archaeological sites; question marks, (?), represent sight records or similar records where the animal was not acquired. The specimen record from Westmoreland County represents individuals obtained from introduced stock.

the beaver population to spread throughout the Commonwealth (Luttringer, 1933).

The first trapping season opened by the Pennsylvania Game Commission for beaver was in 1934. In 50 of 67 counties, a total of 6455 beaver were harvested for that year.

Canis latrans—coyote

The status of coyotes is considered undetermined in Pennsylvania. *Canis latrans* has been referred to as the brush wolf, prairie wolf, eastern coyote, and coyote (Enders, 1985). It has been confused with the wolf (*C. lupus*) and variations of the domestic dog (*C. familiaris*). Although the number of coyote-like canids has been increasing (McGinnis, 1979), confirmation of valid coyote specimens is less common. Many of the coyotes reported are domestic dogs or probable hybrids between the coyote and domestic dog; such specimens are often referred to as coydogs.

According to McGinnis (1979), Pennsylvania coyotes will have the following average and range (in parentheses) of measurements (males followed by females; measurements in millimeters): total length, 1288.0 (1180–1400), 1245.6 (1200–1321); tail length, 360.7 (330–406), 355.0 (325–368); hind foot length, 209.8 (175–233), 199.3 (190–213); length of ear, 113.3 (109–120), 110.3 (105–113); length of skull, 205.0 (179.0–219.0), 197.3 (168.7–213.4); width of skull, 106.2 (100.4–113.3), 103.0 (91.3–113.6). Although these measurements may be helpful for identification purposes, a complete skull is needed for a more conclusive identification. For those individuals that have been trapped or wounded and the head crushed to kill the animal, identification is more difficult, if not impossible. McGinnis (1979) recognized the size and shape of anterior premolars and second upper molars, shape of auditory bullae, shape of frontal shields, presence of a dewclaw, characteristics of pelage, and seasonal breeding cycle to be among useful features of distinguishing *C. latrans* from other *Canis.*

Canis latrans has been reported in Pennsylvania from the Pleistocene (Kurtén and Anderson, 1980; McGinnis, 1979). However, its occurrence has not been continuous since that time. Although skeletal parts of this species are often difficult to differentiate from other *Canis,* no verified records of *C. latrans* are present from Recent paleo-archaeological sites in Pennsylvania (McGinnis, 1979). Apparently the occurrence of the coyote in the Commonwealth has been a relatively recent event, possibly within the past 75 years.

The circumstances surrounding the presence of *C. latrans* in Pennsylvania is open to speculation. There is no question that it does occur in the Commonwealth at the present time. Dr. J. L. George of The Pennsylvania State University estimates the population of coyotes in Pennsylvania to be about 200 (B. Webster, Pittsburgh Post Gazette, 10 Mar 1981). Its occurrence may be explained as either 1) natural migration from the western states, 2) natural migrations from the north (New York, New England, Ontario, and Quebec), or 3) establishment of individuals that were brought into Pennsylvania (or adjacent states) and subsequently escaped or were released. It may be possible that each of these sources contributed to the present occurrence of the species in Pennsylvania. There are arguments supporting all of these possibilities. In any case, the opening of forested areas, availability of domestic prey species, and elaboration of highway systems made it easier for the coyote to become established and spread throughout Pennsylvania.

In the United States the eastern migration of the coyote has been documented. Young and Jackson (1951) indicated the eastern range of *C. latrans* to include Michigan, most of Indiana, and the northwestern corner of Ohio. Mumford and Whitaker (1982) reported the coyote

Table 2.—*Paleontological, historical, and specimen records of "coyotes" in Pennsylvania.*

Date	Locality	Comments	References
		PALEONTOLOGICAL RECORD	
Pleistocene	Blair Co., Frankstown Cave	1 mandible	McGinnis, 1979
		HISTORICAL RECORDS	
1880	McKean Co., Lewis Run	1 shot by Mr. Ives; identification questioned by local hunters	McGinnis, 1979; Shoemaker, 1917
1890	Potter Co.	1 "wolf" killed by J. Razey; assumed to be escaped coyote of Col. Parker that originated in Colorado	McGinnis, 1979; Shoemaker, 1917
1896	Tioga Co.	3 killed; believed to be coyotes originating in western U.S. before being used in carnival	Rhoads, 1903; Savage, 1970; Warren, 1897*b*
Late 1890's	McKean Co., Bradford	4 of 5 young coyotes killed after escaping captivity	McGinnis, 1979
1906	Bedford Co.	1 "prairie wolf" killed	McGinnis, 1979
1907	Blair Co., Flowing Spring	1 "wolf" killed by S. C. Long; CM 1521; later identified as *C. latrans,* (possibly from Mexico or Central America) that probably escaped from captivity	Anon., 1934*b*; Harrison, 1948*b*; McGinnis, 1979; Seton, 1929*a*
1915	Clinton Co.	A. B. Winchester killed 1 coyote	Shoemaker, 1917
1916	Clinton Co.	A. Saxton killed 1 coyote	Shoemaker, 1917
1933	Allegheny Co., Murdocksville Woods	1 "timber wolf" shot by J. H. Wherry; newspaper photograph shows possible coyote	Unreferenced newspaper in files at Carnegie Museum of Natural History
1934	Bradford Co., near Campton	"A pair of coyotes escaped from a tourist camp"	McGinnis, 1979
1934	Washington Co., Hanover Twp.	2 "wolves" killed by F. Cain and J. W. Berry; possibly from pack that es-	Anon., 1934*a*; Harrison, 1948*b*; McGinnis, 1979

Table 2.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
		caped from captivity; both are possible coydogs	
1936	Venango Co., North Sandy	1 killed by dogs	McGinnis, 1979
1937–1938	Wyoming Co., Lane Hill, near Tunkhannock	1 killed by hunter	Anon., 1938*a*; McGinnis, 1979
About 1938	Elk Co., N of Ridgeway	1 young coyote captured alive	Anon., 1938*b*
1938	McKean Co., Owl's Nest	2 captured alive; identification verified by officials of the Biological Survey, Washington, D.C. and the Philadelphia Academy of Sciences	Anon., 1938*c*; McGinnis, 1979
1939	Bradford Co., Sheshequin Twp.	1 collected by G. Shaffer; (ANSP 20071); identified at Philadelphia Academy of Sciences as being similar to *C. l. latrans*	McGinnis, 1979; Ulmer, 1949
1942	Philadelphia Co., Philadelphia, Chestnut Hill	1 trapped by R. Morgan; ANSP 20630; similar to *C. l. estor* (=*mearnsi*)	McGinnis, 1979; Ulmer, 1949
1943	Warren Co., Allegheny National Forest, near Heart's Content	1 killed by hunter	McGinnis, 1979
1943–1945	Bradford Co., northwestern part	At least 7 trapped	McGinnis, 1979
1944	Forest Co.	1 killed by hunter	McGinnis, 1979
1945	Clinton Co., Sumner's Mt., near Linglestown	1 shot by D. F. N. Felty	McGinnis, 1979
1946	Beaver Co., near New Galilee	1 killed by F. McChesney	Harrison, 1948*b*; McGinnis, 1979; McGregor, 1947
1946	Clearfield Co., Goshen Twp.	1 shot and initially identified as a "shepard dog," McGinnis (1979) recognized it as being "the first in-	McGinnis, 1979

Table 2.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
		disputable eastern type coyote occurrence in the state"	
1946	Forest or Venango Co., near Tionesta	1 killed	Harrison, 1948*b*; McGinnis, 1979
1946	Philadelphia Co., Philadelphia, Manayunk	1 captured in store and deposited in Philadelphia Zoo; apparently escaped from captivity	McGinnis, 1979; Ulmer, 1949
1947	Elk Co., Allegheny National Forest, Ervine Run, 3 mi N Hallton	1 killed by hunter	McGinnis, 1979
1947	Forest Co., Allegheny National Forest, near Durhams Siding	1 trapped; CM 25057	McGinnis, 1979; Richmond and Rosland, 1949
1947	Luzerne Co., State Game Land No. 57	1 killed	McGinnis, 1979
1952	Carbon Co., Weatherly	1 trapped by J. Meyers	Kitchen, 1952
1952	Wyoming Co., Forkstown Twp., State Game Lands No. 57	1 killed by member of I. D. Lingle hunting camp	McGinnis, 1979; Meehan, 1953
1954	Greene Co.	1 trapped by G. Kughn	Cowden, 1955
1954	Monroe Co., State Game Lands No. 127	3 killed by L. Schweitzer, L. Matchko, and another hunter, all independent of one another	Spencer, 1955
1954	Potter Co., Nelson Run	1 killed	McGinnis, 1979
1956	Lebanon Co., Indiantown Gap	1 shot by J. Hess	McGinnis, 1979
1957	Clearfield Co., State Game Land No. 34, headwaters of Gifford Run	1 killed by M. H. Yost	Carlson, 1958; McGinnis, 1979
1957	Monroe Co.	1 trapped, filmed, and allowed to escape by D. M. Bush	Doebling, 1957; McGinnis, 1979
About 1962	Lancaster Co., southeastern part	1 killed	McGinnis, 1979
1963	Northampton Co.	1 killed; originated	McGinnis, 1979

Table 2.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
		from a California animal dealer	
1964	Westmoreland Co.	1 killed	McGinnis, 1979
1966	Franklin Co., south of Fannettsburg	1 killed by truck	McGinnis, 1979
1969	Westmoreland Co.	1 killed	McGinnis, 1979
1975	Montgomery Co.	1 killed; possibly an imported animal from the Dakotas	McGinnis, 1979
1978	Centre Co., Rebersburg	1 killed; possibly an imported animal from southern Texas or Mexico	McGinnis, 1979
		SPECIMEN RECORDS (extracted from McGinnis, 1979)	
1907	Blair Co., Flowing Spring	Skin and skull; believed to be imported (McGinnis, 1979)	CM 1522; Carnegie Museum of Natural History
1934	Beaver Co., Hanover Twp., 7 mi W Clinton	Skin, skull, and skeleton	CM 8588; Carnegie Museum of Natural History
1939	Bradford Co.	Believed to be imported (Ulmer, 1949)	ANSP 20071; Philadelphia Academy of Sciences
1942	Philadephia Co.	Believed to be imported (Ulmer, 1949)	ANSP 20630; Philadelphia Academy of Sciences
1946	Clearfield Co.	Possesses characteristics of other *Canis* species	USNM 275155; U.S. National Museum of Natural History
1947	Forest Co., near Durhams Siding	Skin and skull	CM 25057; Carnegie Museum of Natural History
1947	Luzerne Co., Ross Twp., State Game Land No. 57	Skull only	CM-DC 833; Carnegie Museum of Natural History
1952	Wyoming Co.	Possesses characteristics of other *Canis* species	USNM 287333; U.S. National Museum of Natural History
1956	Pike or Monroe Co., near Canadensis	Skull only	CM 39891; Carnegie Museum of Natural History

Table 2.—*Continued.*

Date	Locality	Comments	References
	SPECIMEN RECORDS (extracted from McGinnis, 1979)		
1959	Cameron Co.	Possesses characteristics of other *Canis* species	CM 61371 (DC 1002); Carnegie Museum of Natural History
1960's	Northumberland Co.	Possesses characteristics of other *Canis* species	W. E. Ditty, Selinsgrove, Pennsylvania
1960–1965	Union Co.	Possesses characteristics of other *Canis* species	W. E. Ditty, Selinsgrove, Pennsylvania
About 1963	Lehigh-Northampton cos.		Pennsylvania Game Commission, Harrisburg
1963	Potter Co.	Possesses characteristics of other *Canis* species	USNM 288970; U.S. National Museum of Natural History
1963	Tioga Co.	Possesses characteristics of other *Canis* species	USNM 288845; U.S. National Museum of Natural History
1964	Elk Co., Ridgeway Twp., W Rt 948, ¼ mi N Ridgeway	Skull only	CM 66775; Carnegie Museum of Natural History
1964	Westmoreland Co., near Ligonier	Skin and skull; possesses characteristics of other *Canis* species	CM 40166; Carnegie Museum of Natural History
1965	Cumberland Co., 1 mi N Carlisle	Skull only	CM 61393 (DC 1239); Carnegie Museum of Natural History
1965	Elk Co., Benzinger Twp.	Skull only	CM 40581; Carnegie Museum of Natural History
1968	Bradford Co.	Possesses characteristics of other *Canis* species	C. Cass
1969	Erie Co.	Possesses characteristics of other *Canis* species	PSU-HJM 27; Penn State University
1969	Westmoreland Co.	Possesses characteristics of other *Canis* species	CM 59551 (DC 1378); Carnegie Museum of Natural History
1970	Bradford Co., Warren Twp.	Skin, skull, and body skeleton; all possess characteristics of	CM 61433 (8230); CM 61434 (8231); Carnegie

Table 2.—*Continued.*

Date	Locality	Comments	References
		SPECIMEN RECORDS (extracted from McGinnis, 1979)	
		other *Canis* species	Museum of Natural History; B. Holden, South Apalachin, New York
1970	Susquehanna Co.	Skull only; possesses characteristics of other *Canis* species	CM 59582 (DC 1437); Carnegie Museum of Natural History
1971	Clinton Co.		PSU-HJM 38; Penn State University
1972	Clinton Co.	Possesses characteristics of other *Canis* species	PSU-HJM 72; Penn State University
1974	Bradford Co.	Possesses characteristics of other *Canis* species	A. D. Rockwell, Sayre, Pennsylvania
1974	Centre Co.		PSU-HJM 22; Penn State University
1974	Potter Co.	Possesses characteristics of other *Canis* species	P. Olphin, Red Lion, Pennsylvania
1974	Schuylkill Co.	Possesses characteristics of other *Canis* species	D. Bonawitz, Pine Grove, Pennsylvania
1974	Tioga Co.	Possesses characteristics of other *Canis* species	PSU-HJM 21; Penn State University
1975	Beaver Co.	Possesses characteristics of other *Canis* species	PSU-HJM 23; Penn State University
1975	Bradford Co.	Possesses characteristics of other *Canis* species	PSU-HJM 75; Penn State University
1975	Centre Co.		PSU-HJM 44; Penn State University
1975	Clarion Co.	Both possess characteristics of other *Canis* species	PSU-HJM 25; PSU-HJM 37; Penn State University
1975	Clearfield Co.	Both possess characteristics of other *Canis* species	PSU-HJM 33; PSU-HJM 39; Penn State University
1975	Luzerne Co.	All possess characteristics of other *Canis* species	PSU-HJM 26; PSU-HJM 35; PSU-HJM 43; Penn State University

Table 2.—*Continued.*

Date	Locality	Comments	References
		SPECIMEN RECORDS (extracted from McGinnis, 1979)	
1975	Mifflin Co.	Possesses characteristics of other *Canis* species	PSU-HJM 32; Penn State University
1975	Montgomery Co.		B. J. Schmader, Collegeville, Pennsylvania
1975	Wayne Co.	Possesses characteristics of other *Canis* species	PSU-HJM 36; Penn State University
1976	Bradford Co.	Possesses characteristics of other *Canis* species	PSU-HJM 50; Penn State University
1976	Carbon Co.	Possesses characteristics of other *Canis* species	PSU-HJM 47; Penn State University
1976	Crawford Co.	Possesses characteristics of other *Canis* species	PSU-HJM 73; Penn State University
1976	Lebanon Co.	Possesses characteristics of other *Canis* species	PSU-HJM 48; Penn State University
1977	Armstrong Co.	Possesses characteristics of other *Canis* species	PSU-HJM 58; Penn State University
1977	Butler Co.		PSU-HJM 67; Penn State University
1977	Carbon Co.	Possesses characteristics of other *Canis* species	PSU-HJM 56; Penn State University
1977	Clinton Co.	Possesses characteristics of other *Canis* species	1007; Galeton Area High School
1977	Cumberland Co.		PSU-HJM 49; Penn State University
1977	Crawford Co.	Possesses characteristics of other *Canis* species	PSU-HJM 66; Penn State University
1977	Dauphin Co.		PSU-HJM 64; Penn State University
1977	Lawrence Co.	Possesses characteristics of other *Canis* species	PSU-HJM 57; Penn State University
1977	Lycoming Co.	Possesses characteristics of other *Canis* species	PSU-HJM 53; Penn State University
1977	Potter Co.	Both possess characteristics of other *Canis* species	1001; 1006; Galeton Area High School

Table 2.—*Continued.*

Date	Locality	Comments	References
		SPECIMEN RECORDS (extracted from McGinnis, 1979)	
1977	Tioga Co.	Possesses characteristics of other *Canis* species	PSU-HJM 65; Penn State University
1977	Westmoreland Co.	Possesses characteristics of other *Canis* species	PSU-HJM 63; Penn State University

inhabited only the prairie habitats of Indiana prior to the settlement of the state. The species currently has a statewide distribution in Indiana, but is not considered common (Mumford and Whitaker, 1982). In Michigan, the coyote was reported by the state conservation department (1927–1928) to be absent from the Lower Peninsula, but now occurs "sporadically" in southern Michigan (Baker, 1983). The eastern migration into Ohio is not well documented because of relatively few records. Gottschang (1981) reported that the first validated record for

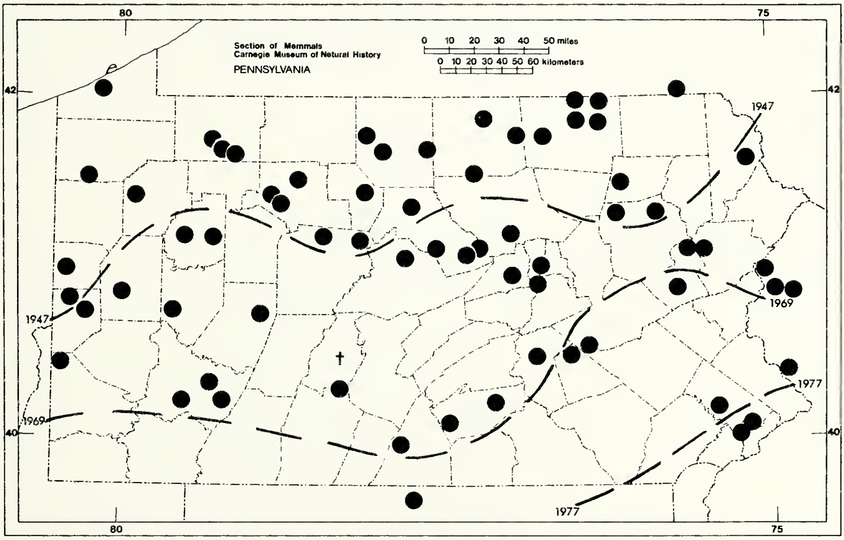

Fig. 2.—Map of Pennsylvania showing location of records of "coyotes" in the Commonwealth. Broken lines represent possible progression of distribution, but the actual history has been complicated with the presence of introduced animals (extracted from verified records from McGinnis, 1979).

that state was from Preble County in 1947. Subsequent records for Ohio included a few additional records from various parts of the state (Frantz, 1955; Gottschang, 1981). McKeever (1954) reported one verified specimen of coyote from West Virginia and assumed that it escaped from captivity. Paradiso (1966) reported two specimens from Maryland taken in 1921 and 1961. He suggests that at least the 1921 record, and possibly both records, represent animals that escaped from captivity. Assuming the early records represent introductions, records from Indiana, Michigan, Ohio, West Virginia, and Maryland suggest that a migration into Pennsylvania from the west could have been started in the 1940's but only by a restricted number of individuals. The lack of additional verified records throughout the states south and west of Pennsylvania, and the noticeably greater number and earlier records from Pennsylvania (Table 2), raises some question as to the actual history of a possible migration from the west.

The possibility of coyotes migrating from the north is supported by the natural migrations into eastern Canada. Banfield (1974) reported that "coyotes started to move eastward across northern Ontario, and between 1918 and 1948 they occupied all of central and southern Ontario and western Quebec." Then the species migrated into New York and New England from the St. Lawrence Valley (Banfield, 1974). Warfel (1937) indicated coyotes were in Massachusetts and New York prior to 1936. Frantz (1955) reported that "New York has been cognizant of them since the middle thirties." The population of coyotes in New York is large and well established, as indicated by an estimated harvest of 3000 coyotes during 1975–1976 (McGinnis, 1979). Migrations of coyotes from a large population in New York as early as the 1930's could explain several of the early records in Pennsylvania (Table 2).

Although *C. latrans* may have migrated naturally into Pennsylvania, the possible influence of introduced individuals cannot be neglected. Shoemaker (1917) reported the killing of a possible pet coyote in 1890 in Potter County. Rhoads (1903) reported two cases of coyotes, or "prairie wolves," in the Commonwealth in 1896 and 1897 in Tioga and Franklin counties, respectively. Both of these cases probably involve imported coyotes. Another coyote was taken in 1907 in Blair County (CM 1522). McGinnis (1979) believes that specimen to have characteristics similar to coyotes from Mexico or Central America, and that it was an animal that escaped from captivity. Although these cases represent scattered events, the practice of bringing coyotes into Pennsylvania and the surrounding region was apparently common. Ulmer (1949) reported specific specimens of coyotes from Pennsylvania and New Jersey resembling different geographic races of *C. latrans*. He also reported that in the 1930's and 1940's the Philadelphia Zoo acquired coyotes from the local community, and also presented coyotes to individuals in the region. Similar practices of keeping captive coyotes were evident throughout the Commonwealth. In 1934, a pair of coyotes escaped captivity in Bradford County (McGinnis, 1979). The same year a resident of Washington County owned a pack of coyotes (possibly coydogs) until the holding pen burned down and the animals escaped (Anon., 1934*a*). McGinnis (1979) also reported some of the southern Pennsylvania records between 1959 and 1969 to be imported animals. It is not certain how many individuals of *C. latrans* may have been brought into the Commonwealth, and how many of those animals, or their offspring, were released or escaped captivity. It is also not known how much influence these animals have had on the current population of *C. latrans* in Pennsylvania. Undoubtedly, there has been some genetic influence as well as a definite contribution to the confusion surrounding the history of the species in the Commonwealth.

McGinnis (1979) suggests that the coyote became scattered across the northern part of the Commonwealth by the 1930's and gradually spread southward into Maryland and West Virginia. The number of records of coyotes in Pennsylvania increased substantially in the 1960's and 1970's (Table 2). McGinnis (1979) indicates the number of coyotes is now increasing throughout the Commonwealth (Fig. 2).

Canis lupus—wolf

Canis lupus in Pennsylvania has commonly been referred to as wolf, but also includes derivatives such as timber wolf, eastern timber wolf, eastern wolf, gray wolf, and Appalachian gray wolf (Allen, 1942; Rhoads, 1903; Seton, 1929*a*; Zegers, 1985). If there is any confusion about this species, it is the result of misidentifying other canids, specifically *Canis latrans* (coyote) and *Canis familiaris* (domestic dog). This confusion has been evident in historical accounts and skeletal remains in paleo-archaeological sites. Wolf remains are among the larger canids encountered. Young and Goldman (1944) give measurements for the greatest length of skull and zygomatic breadth of an adult male wolf from Pennsylvania (ANSP 2261) as being 234.2 mm and 122.4 mm, respectively; the greatest length of skull for an adult female from Pennsylvania (ANSP 2262) was given as 234.8 mm. Although males are typically larger than females, total length, length of tail, and length of hind foot of an adult male will be about 1625 mm, 300 mm, and 250 mm, respectively (Hamilton, 1943).

The pre-Columbian distribution of *C. lupus* in the eastern United States extended as far south as the northeastern corner of Florida (Mech, 1970). Throughout this region the wolf lived in most habitats (Mech, 1970). Paleo-archaeological site records and over 125 historic records (Table 3) indicate that the wolf inhabited all parts of Pennsylvania (Fig.

Table 3.—*Paleo-archaeological, historical, and specimen records of* Canis lupus *from Pennsylvania.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
N.D.	Somerset-Fayette cos.	1 bone fragment	Gilmore, 1946
Pleistocene	Montgomery Co., on Schuylkill R., below Valley Forge, Port Kennedy Cave	10 *Canis* + wolf	Guilday, 1976
Quaternary	Monroe Co., 2½ mi SW Stroudsburg, Hartmans Cave (=Crystal Hill Cave)	Skeletal parts	Leidy, 1889
Post-Wisconsin to Recent	Bedford Co., West St. Clair Twp., 1.5 mi NE New Paris	Skeletal parts representing 2 individuals	Guilday and Bender, 1958
11,300 ± 700 BP	Washington Co., Jefferson Twp., Meadowcroft Rockshelter (36Wh297)	1 skeletal part representing 1 individual	Guilday et al., 1980
pre-4000 BC	Huntingdon Co., W bank Raystown Branch of Juniata R., Sheep Rockshelter (36Hu1)	3 skeletal parts representing 1 individual	Guilday and Parmalee, 1965
100 BC–900 AD	Venango Co., Sandy Creek Twp., 3 mi SE Franklin, Quaker State Rockshelter (36Ve27)	3 skeletal parts	Guilday and Tanner, 1962
1875 ± 100 BP	Bedford Co., near New Paris, Sinkhole No. 4	Skeleton	Guilday et al., 1964
1190 AD	Somerset Co., Summit Twp., Gnagey Site (36So55)	3 skeletal parts	George, 1983
1330 AD	Allegheny Co., McKees Rocks Village Site (36Al16)	3 skeletal parts representing 1 individual	Lang, 1968
1600–1625 AD	Lancaster Co., Washington Boro, 3 mi S Columbia, Eschelman Site (36La12)	39 skeletal parts representing 4 individuals	Guilday et al., 1962
	HISTORICAL RECORDS		
1677	Lawrence Co., New Castle	55 bounties paid	Hazard, 1850
1722	Lancaster Co., few mi below Lancaster	S. Atkinson collected 2 bounties	Ellis and Evans, 1883
1759	Westmoreland Co.,	Account by J. Kenny	Harpster, 1938

Table 3.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
	Ligonier	about 6 men eaten by wolves	
1760	Snyder Co.	109 killed in community hunt led by "Black Jack" Schwartz	Shoemaker, 1917
1772	Allegheny Co., Braddock	Rev. D. McClure comments about wolf damage following an Indian massacre	Harpster, 1938
1780	Chester Co., Valley Forge	Report of last wolf killed	Pennypacker, 1872
1799	Luzerne Co., Wilkesbarre	Bounties paid	Harvey, 1927
1800	Bucks Co., Plumstead	1 captured by J. Smith	Rhoads, 1903
1800–1805	Susquehanna Co.	7–8 killed by Sabin	Blackman, 1873
1801–1803	Luzerne Co., Wilkesbarre	Bounties paid annually	Harvey, 1927
1803	Butler Co.	8 bounties paid	Webb and Stevens, 1934
1805	Bradford Co.	90 killed in a community hunt	Heverly, 1926
1806	Luzerne Co., Wilkesbarre	Bounties paid	Harvey, 1927
1803–1808	Armstrong-Westmoreland cos.	Bounties paid annually	Smith, 1883
1807–1840	Butler Co.	Bounties paid on 170 wolves	Webb and Stevens, 1934
1814	Bradford Co.	Bounties paid	Bradsby, 1891
1816	Chester Co., West Nottingham	1 killed	Lancaster J., 22 Jan 1816; Rhoads, 1903; Watson, 1844
1817	Bradford Co.	1 killed by A. Price	Perkins, 1870
1818	Bradford Co.	50 killed during a community hunt of 1000 men organized by A. Stevens	Warren, 1897*b*
1818	Bradford Co., Waverly	13 killed during a community hunt	Warren, 1897*b*
1826	McKean Co.	R. Cory and R. Hill collected bounties	Leeson, 1890
1830	Huntingdon Co., ½ mi from Huntingdon	1 "black wolf" killed	Harrisburg Argus, 25 Dec 1830; U.S. Gazette, 21 Dec 1830

Table 3.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1830	Berks and Schuylkill cos.	14 killed during a community hunt	Shoemaker, 1917
1830	Clinton Co.	1 killed by G. Quiggle	Shoemaker, 1929
1831	Huntingdon Co.	7 bounties paid	Hazard, 1832
1831	York Co., vicinity Rosstown (=Rossville)	1 killed by H. O'Hail	Hazard, 1831*a*
1831	Lancaster Co., Conestoga Twp.	1 killed	Berks and Schuylkill J., 26 Mar 1831
1832	Centre Co., Bellefonte	13 killed by B. Long	Democratic Inqu., 20 Dec 1832; Watson, 1844
1834	Sullivan Co.	Bounties paid	Rhoads, 1903
1834–1835	Union Co., Buffalo Mt., Shade Mt., near Swinefordstown	20 found frozen	Shoemaker, 1917
1835	Clearfield Co.	B. Long collected young from five dens	Walker, 1960*a*
1835	Luzerne Co., Lackawanna Valley, Jefferson	1 killed by Mrs. J. Cobb with pitchfork; bounty collected	Hollister, 1869
1836	Perry Co., Liberty Valley	Man killed by wolves; 6 wolves killed in fight	Watson, 1844
1840	Butler Co.	1 killed by A. McCandless, bounty paid; reported to be last bounty in county	Webb and Stevens, 1934
1843	Potter Co., Oleona	Mrs. F. French treed by wolves, 5 of which were killed	Beebe, 1934
1847	Potter Co.	Bounties paid	Beebe, 1934
1848	Wayne Co.	1 killed by W. T. Teeple reported to be last killed in county	Rhoads, 1903
1850	Fayette Co., Salt Lick Twp.	1 killed	Grimm and Roberts, 1950
1855	Forest Co., Hemlock Cr.	1 killed	Rhoads, 1903; Savage, 1970
1855	Philadelphia Co., lower part Philadelphia	1 killed by farmers	Wilkesbarre Advocate, 16 May 1855
1856	Clearfield Co.	12 killed by J. Berfield and H. Mason	Shoemaker, 1917

Table 3.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1857	Union Co., Weikert Run	W. Moyer, B. Pursley, and J. F. Barnett killed 11 "black wolves"	Shoemaker, 1917
1858	Clearfield Co., near Janesville	1 killed by A. Neverling	Rhoads, 1903; Savage, 1970; Warren, 1897*a*
1858	Cambria Co., 4 mi N Ebensburg	1 trapped by J. L. Williams	Daily Telegraph, 18 Aug 1858
1859	Clearfield Co.	1 "black wolf" killed	Daily Telegraph, 10 Jan 1859
1859	Cambria Co.	2 captured	Daily Telegraph, 14 Mar 1859
1859	Centre Co., Snow Shoe Region	12 poisoned by T. Askey	Shoemaker, 1917
1860	Sullivan Co.	1 killed by R. Williams; reported to be last killed in county	Rhoads, 1903
1860	Westmoreland Co., Chestnut Ridge	1 killed	Grimm and Roberts, 1950
1861	Clinton Co., Wayne Twp.	1 female and at least 6 young killed by J. Earon	Shoemaker, 1917, 1929
About 1865	Berks Co., Albany Twp.	1 killed by I. Hein; reported to be last killed in township	Poole, 1932
1865	Warren Co.	Several killed by Faddy boys	Shoemaker, 1917
1866	Warren Co.	J. Irvin collected 1 bounty; last issued by county	Shoemaker, 1917; Walker, 1960*a*
1867	Indiana Co.	1 killed	Patriot and Union, 17 May 1867
1867	Lycoming-Sullivan county line	1 killed by S. Batlin, H. Williams, and L. D. Porter	Tomkins, 1931
1868	Clarion Co., Licking Cr. Valley	G. Rittenhouse was chased by wolves; 1 killed	True Democrat, 2 Dec 1868; Morning Patriot, 8 Dec 1868
1868	McKean Co., Cole Cr.	4 captured by L. Lyman and J. W. Stark	Rhoads, 1903; Savage, 1970
1868	McKean Co.	Bounty paid	Savage, 1968; Walker, 1960*a*
1869	McKean Co., W Potato Cr.	7 caught by C. W. Dickinson	Rhoads, 1903; Savage, 1970

Table 3.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1870	Wyoming Co.	1 killed by O. B. Vose; reported to be last record in county	Grimm and Roberts, 1952; Rhoads, 1903
About 1870	Clinton Co.	1 killed by A. Vallon	Shoemaker, 1929
1870	Clinton Co., near Dunnsburg	Grugan killed "stray" wolf	Shoemaker, 1929
1870	McKean Co.	1 caught by C. W. Dickinson	Rhoads, 1903; Savage, 1970
1870	Somerset Co., Rockwood	1 killed by Livengood	Grimm and Roberts, 1950
1871	Elk Co.	J. R. Green collected 1 bounty	Shoemaker, 1917
1871	Erie Co.	1 killed (120 lb); believed to be escaped wolf	Daily Patriot, 24 April 1871
1871	McKean Co.	1 caught by C. W. Dickinson	Rhoads, 1903
1872	Lycoming Co., few miles from Ralston	1 killed by L. Kissenger	Tomkins, 1931
1872	McKean Co.	1 caught by C. W. Dickinson	Rhoads, 1903
1872	McKean Co.	8 caught by C. W. Dickinson	Rhoads, 1903; Savage 1970
1872	Chester Co., Valley Forge	Last wolf killed according to Pennypacker	Shoemaker, 1917
1873	Elk Co.	J. Bennett, Jr. collected 1 bounty	Shoemaker, 1917
1874	Blair Co., near Tyrone	1 captured	Harrisburg Evening Mercury, 4 April 1874
1874	Clarion Co., Farmington Twp.	1 killed	Daily Patriot, 10 Aug 1874
1874	Elk Co.	A. J. Rummer, J. R. Green, J. Myers, and C. A. Brown each collected 1 bounty	Shoemaker, 1917
1874	Elk Co.	G. Smith collected 2 bounties	Shoemaker, 1917
1874	Potter-Tioga Co. line, waters of Phoenix and Pine crs.	1 killed	Leeson, 1890
1874	Tioga Co., Laurel Hill	1 killed by L. Kissenger; may be same as 1872, Lycoming Co., account	Savage, 1970

Table 3.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1874	Blair Co., near Tyrone	1 captured	Harrisburg Evening Mercury, 4 April 1874
1875	Potter Co.	1 killed by L. Lyman	Rhoads, 1903; Savage, 1970; Shoemaker, 1917
1876	Clearfield Co., Union Twp.	2 captured	Raftsman's J., 22 Mar 1876
1877	Clearfield Co., 1 mi from Pennfield	1 with 5 young seen; 5 young captured	Globe, 5 Jun 1877
1877	Clinton Co.	1 killed by J. Hamersley; reported to be last killed in county	Shoemaker, 1917
1877	Elk Co.	O. B. Fitch collected 1 bounty	Savage, 1968; Shoemaker, 1917; Walker, 1960*a*
1877	Lehigh Co.	1 "red wolf" killed; first in 70 years	Daily New Era, 11 May 1877
1878	Allegheny Co., Clinton	2 killed	Daily New Era, 13 Jul 1878
1878	Cambria Co., Cambria Twp.	1 captured by G. J. Lloyd	Huntingdon J., 18 Oct 1878
1878	Cambria Co., Blacklick Twp.	1 killed	York Daily, 17 Oct 1878
1878	Clearfield Co., Pike Twp.	1 killed by J. T. Hartshorne	Raftsman's J., 18 Dec 1878
1878	McKean Co.	Many poisoned by Griffins and C. W. Dickinson	Shoemaker, 1917
1879	Armstrong Co., Blacklick Twp.	Several poisoned	Snyder Co. Tribune, 10 April 1879
1879	Cambria Co., few mi from Cresson	1 captured	Globe, 28 May 1879
1879	Indiana Co.	2 captured by Mr. Ripple	Raftsman's J., 9 April 1879
1880	Cambria Co., Barr Twp.	13 killed by Brown	Globe, 17 Mar 1880; Harrisburg Telegraph, 8 May 1880
1881	Clearfield Co.	Bounty paid	Savage, 1968; Walker, 1960*a*
1881	Jefferson Co.	2 killed by A. Long; reported to be last killed in county	Shoemaker, 1917
1881	Clearfield Co.	2 killed by J. Long	McKnight, 1905*a*
1882	Border Mifflin, Juniata, and Huntingdon cos.	1 killed; first in 15 years	Shippensburg News, 16 Dec 1882

Table 3.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1884	Clearfield Co.	5 killed by S. I. Nelson	Shoemaker, 1917
1884	Forest Co.	1 killed by E. Dobson; reported to be last killed in county	Rhoads, 1903; Shoemaker, 1917
1884	Forest Co.	Bounty paid	Savage, 1968; Walker, 1960*a*
1885	Tioga Co.	1 killed	Rhoads, 1903
1885	Tioga Co.	1 killed by L. Kissinger; questionable record	Shoemaker, 1917
1885	Mifflin Co., Treaster Valley	D. Treaster killed 2 "black wolves"	Shoemaker, 1917
1886	Berks Co.	1 bounty paid	Warren, 1897*b*
1886	Berks Co., Blue Mts.	1 killed by D. Long; last record from Blue Mt.	Shoemaker, 1917
1886	McKean Co., Potato Cr.	1 killed by G. Sizer	Shoemaker, 1917
1886	McKean Co., Kinzua Cr.	1 killed; reported to be last killed in county	Mohr, 1931; Rhoads, 1903
1886	Mifflin Co., Treaster Valley	1 killed by D. Treaster; reported to be last killed in Treaster Valley	Shoemaker, 1913
1886	Mifflin Co., Treaster Valley	D. Treaster killed 1 "black wolf"	Shoemaker, 1917
1886	Tioga Co.	Bounty paid	Savage, 1968; Walker, 1960*a*
1887	Elk Co.	1 killed	Rhoads, 1903
1887	Wayne Co., Prompton, near Honesdale	1 killed by D. Routan; believed to have crossed over from New York	Rhoads, 1903; Shoemaker, 1917
1888	McKean Co., Kinzua Cr.	1 killed by C. Ives and T. Price, maybe 1886	Shoemaker, 1917
1890	Indiana Co., near Black Lick	1 killed; locality and date raise questions about record	Grimm and Roberts, 1950
1890	Potter Co.	1 bounty paid	Warren, 1897*b*
1890	Potter Co.	1 "wolf" reported killed; possibly pet coyote	Shoemaker, 1917
1890	Potter Co.	1 killed by F. Gage, bounty collected;	Harrison, 1948*b*; Shoemaker, 1917

Table 3.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
		reported to be last killed in county	
1890	Potter Co.	1 bounty paid	Rhoads, 1903; Savage, 1970; Walker, 1960*a*
1891	Elk Co.	1 killed	Shoemaker, 1917
1891	Elk Co.	1 killed; reported to be last killed in county	Allen, 1942; Rhoads, 1903; Walker, 1960*a*
1891–1892	Clearfield Co.	1 killed by W. Bonsall; reported to be last killed in county and Commonwealth	Rhoads, 1903; Shoemaker, 1917
1892	Clearfield Co.	2 killed by S. I. Nelson; reported to be possibly last killed in Commonwealth	Harrison, 1948*b*; Shoemaker, 1917; Walker, 1960*a*
1896	Lackawanna Co.	4 bounties paid; questionable records	Rhoads, 1903; Shoemaker, 1917; Warren, 1897*b*
1896	Tioga Co.	3 "wolves" killed; believed to be coyotes originating in western U.S. before being used in carnival	Rhoads, 1903; Savage, 1970; Warren, 1897*b*
1897	Franklin Co., Bear Valley near Louden, Peters Twp.	J. Poole reported killing 1 "wolf"; false record; skin came from coyote, skull came from domestic dog	Rhoads, 1903; Savage, 1970
1897	Somerset Co., Jefferson Twp.	J. Aneer (=Queer) reported to have killed 1 wolf; record is questionable	Rhoads, 1903; Savage, 1970; Shoemaker, 1917; Swank, 1908
1897	Westmoreland Co.	1 killed; believed to have originated in western U.S. and released for hunting	Warren, 1897*b*
1902	Somerset Co., near Laughlentown	V. Eagan reported to have killed 1 wolf; apparent lie (reported to Pittsburgh Paper, 6 Feb 1902)	Rhoads, 1903
1903	Luzerne Co., near Hazelton	1 "wolf" killed by J. Hoffman	Swank, 1908

Table 3.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1907	Blair Co., Flowing Spring	1 "wolf" killed by S. C. Long; CM 1521; later identified as *C. latrans*	Anon., 1934*b*; Harrison, 1948*b*; McGinnis, 1979; Seton, 1929*a*
1907	Border Cambria and Blair cos., Portage Twp.	1 "wolf" killed	Shoemaker, 1917
1908	Greene Co.	1 "wolf" killed	Swank, 1908
1908	Luzerne Co., near Hazelton	1 killed	Swank, 1908
1914		1 "brown wolf" killed by D. Long	Poole, 1932
1924	Lackawanna Co., Clarks Summit, 8–13 mi W. Scranton	1 "wolf" shot by S. Billings	Unreferenced newspaper in files at Carnegie Museum of Natural History
1933	Allegheny Co., Murdocksville woods	1 "timber wolf" shot by J. Wherry	Unreferenced newspaper in files at Carnegie Museum of Natural History
1946–1947	Venango Co., Oil City	1 "wolf" caught by M. Irwin; later identified as a feral dog	Harrison, 1948*b*
1946	Forest Co., near Tionesta	1 "wolf" killed by L. Coleman; identification never verified	Harrison, 1948*b* Pittsburgh Sun Telegraph, 14 Dec 1946
1948	Warren Co., Kinzua-Corydon	1 reported shot by L. Shafer; rumor spread as a result of Shafer destroying wolves at the McCleary Wolf Farm	Harrison, 1948*b*; Pittsburgh Sun Telegraph, 14 Dec 1946
		SPECIMEN RECORDS	
Pre-1859	Locality unknown	Skull presented by Dr. Morton	ANSP 2261; Philadelphia Academy of Sciences
Pre-1859	Locality unknown	Skull presented by Dr. Morton; extensive toothwear suggests captivity	ANSP 2262; Philadelphia Academy of Sciences

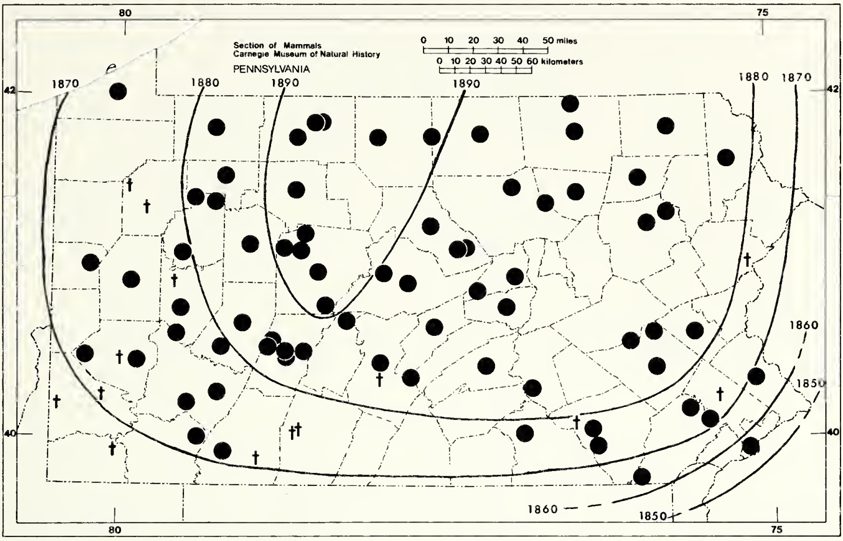

Fig. 3.—Map of Pennsylvania showing location of records and possible distribution of *Canis lupus* before it was extirpated. Symbols used are described in Fig. 1.

3) and probably in substantial numbers, at least until the mid-1800's. As early as 1677 New Castle in Lawrence County paid 55 wolf bounties (Hazard, 1850). In 1770 Pennsylvania exported 6581 wolf skins for the fur trade (Savage, 1968; Walker, 1960*a*). Seton (1929*a*) estimated that in early colonial times, the wolf population in Pennsylvania was about 40,000. Throughout the 1700's and 1800's the wolf was heavily persecuted. Community hunts were popular and accounted for rapid extirpation of local populations. Accounts have described the killing of 50 to over 100 wolves in a single hunt (Heverly, 1926; Shoemaker, 1917; Warren, 1897*b*). In addition to community hunts the numbers of wolves were reduced further through general hunting and trapping, poisoning, and bounty systems. The latter methods became the dominant means of control by the mid-1800's. After 1850 the distribution of the wolf in Pennsylvania began a noticeable regression (Fig. 3). With each passing decade the historical reports of wolves constricted geographically toward the northcentral region of the Commonwealth. Between 1880 and 1890 the distribution was significantly reduced. After 1890 the wolf was restricted to McKean, Potter, Elk, Clearfield, and possibly Cameron counties.

The last record of wolf in Pennsylvania has been disputed (Harrison, 1948; Rhoads, 1903; Shoemaker, 1917; Walker, 1960*a*). This confusion has been primarily caused by misidentification of other canid species and fraud. If the receding distribution of the species can provide any indication of where the last records might be found, it is likely that this last record of a naturally occurring wolf in Pennsylvania was in Clearfield County in 1892. Many of the subsequent records were proven erroneous, fraudulent, or from illogical locations (see Table 3).

The occurrence of the wolf in Pennsylvania changed from an extensive distribution with probably large numbers, to extirpation during a 50–75 year time period. Unfortunately, only two specimens were ever deposited in research collections.

After the wolf disappeared from Pennsylvania, the distribution of the natural population receded to Ontario and Quebec (Mech, 1970). It is not likely that *C. lupus* will ever inhabit Pennsylvania again.

Gulo gulo—wolverine

Gulo gulo is known by the common names of wolverine, glutton, skunk-bear, and carcajou (Allen, 1942; Rhoads, 1903; Seton, 1929*b*; Shoemaker, 1929). The species was considered rare in Pennsylvania when it existed (Rhoads, 1903) and, therefore, was not familiar to many people. The wolverine is blackish brown in coloration and has a distinctive light brown stripe on the sides. Total length and tail length of males is 900–1125 mm and 190–260 mm, respectively. Females are about 10% smaller (Hall, 1981).

The wolverine is most commonly associated with "boreal evergreen forests and barrens" (Allen, 1942). The species is solitary in behavior and tends to avoid areas of human activity, thus it soon disappeared as more settlements developed (Allen, 1942).

During historical times the southern distributional limit of the wolverine in the eastern United States was northern Pennsylvania (Table 4; Fig. 4). This distribution is based primarily on an account from Portage Township, Potter County (Rhoads, 1903). Allen (1942) indicated some skepticism about the range extension caused by this record. DeKay (1842) reported "the wolverine was formerly found as far south as Carolina." Paleo-archaeological records from Pennsylvania (Guilday et al., 1980; Kurtén and Anderson, 1980) and Maryland (Gidley and Gazin, 1938) further support the fact that the wolverine occurred in Pennsylvania and that its distribution may have included the entire Commonwealth. During historical times the distribution of *G. gulo* in Pennsylvania may have been restricted to the northcentral region in the vicinity of McKean, Potter, Tioga, and Clinton counties. Rhoads (1903) commented about the wolverine possibly being in western Pennsylvania. A record from the vicinity of Toledo, Ohio, in 1842 (Brayton, 1882) may support that contention.

Table 4.—*Paleo-archaeological and historical records of* Gulo gulo *from Pennsylvania.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
Pleistocene	Montgomery Co., on Schuylkill R., below Valley Forge, Port Kennedy Cave	Skeletal parts representing 4 individuals	Cope, 1871, 1899; Rhoads, 1903
11,300 ± 700 BP	Washington Co., Jefferson Twp., Meadowcroft Rockshelter (36Wh297)	1 skeletal part representing 1 individual	Guilday et al., 1980
	HISTORICAL RECORDS		
N.D.	Potter Co., Pine Cr.	C. C. Burdette reported killing 1 wolverine	Rhoads, 1903
1846	Mercer Co.	Occurrence reported in Stokley's "Observations on Mercer Co., Pa."	Rhoads, 1903
About 1858	Potter Co., Portage Twp., near Great Salt Lick	1 trapped by J. Nelson	Allen, 1942; Hall, 1981; Rhoads, 1903
Pre-Civil War	McKean Co. Tuna Cr.	1 killed by J. Logan	Shoemaker, 1919
Pre-Civil War	Tioga Co., Marsh Cr.	1 trapped	Shoemaker, 1919
1863	Potter Co., east fork of Sinnemahoning Cr.	1 trapped by J. P. Nelson; Rhoads (1903) believes this is the same as 1858 record	Mohr, 1931; Rhoads, 1903; Shoemaker, 1919
1862	Locality unknown	J. C. French reported seeing tracks and individual	Shoemaker, 1919
1868	Clinton Co., Penatang	J. Mouillefarine reported killing female and five young	Shoemaker, 1929
1869	Clinton Co.	J. Mouillefarine reported being attacked by wolverine	Shoemaker, 1929
About 1870	Clinton Co.	S. Nelson, Jr. suggested they were in county at that time	Shoemaker, 1929
1871–1876	Locality unknown	J. C. French examined skin of recently killed individual	Shoemaker, 1919
About 1875	Clinton Co.	T. G. Simcox reported last dates of occurrence	Shoemaker, 1929

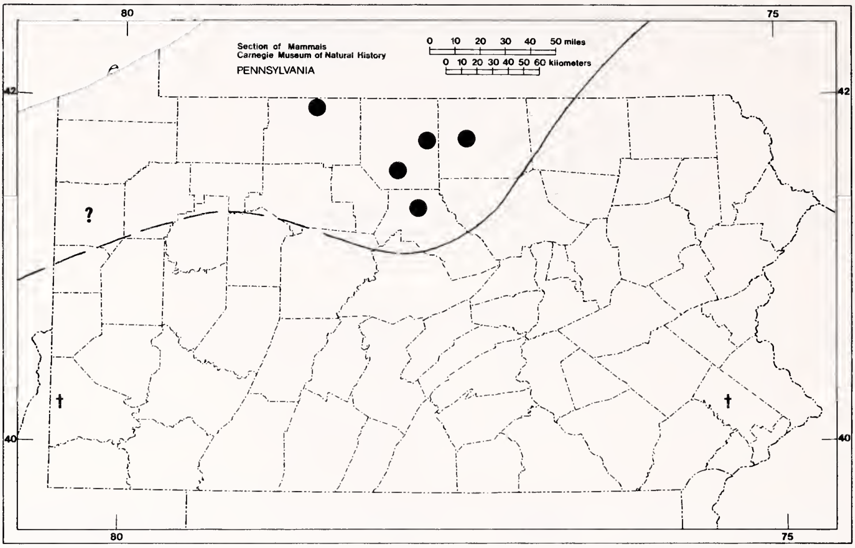
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Fig. 4.—Map of Pennsylvania showing location of records and possible distribution of *Gulo gulo* before it was extirpated. Symbols used are described in Fig. 1.

The 1863 record from Potter County, documented by Rhoads (1903), is the most widely accepted record of wolverine in Pennsylvania. Shoemaker (1919, 1929) published later accounts of specimens from the vicinity of Potter County. Assuming that these records are authentic, it is possible the wolverine was in Pennsylvania until the early 1870's. Since that time the species has receded into northern Quebec and Ontario (Banfield, 1974).

Martes americana—marten

Martes americana has been referred to in Pennsylvania as marten, southeastern marten, Canadian marten, American marten, pine marten, marten cat, American sable, Hudson's Bay sable, and pine weasel (Cunningham, 1985*a*; Rhoads, 1897, 1903; Seton, 1929*b*; Shoemaker, 1929). In the records and references reviewed, there was no apparent confusion of this taxon with other mammal species to suggest questionable accounts. The marten is golden brown in color. The throat and chest are yellowish. Males and females have total lengths of 570–682 mm and 513–560 mm, respectively; tail length is 170–240 mm and 165–195 mm, respectively (Hall, 1981).

It is surprising to find the marten excluded from most paleontological and archaeological records. The only such record in Pennsylvania is from Sinkhole No. 4 near New Paris, Bedford County (Guilday et al.,

Table 5.—*Paleontological, historical, and specimen records of* Martes americana *from Pennsylvania.*

Date	Locality	Comments	References
		PALEONTOLOGICAL RECORDS	
11,300±1000 BP	Bedford Co., near New Paris, Sink Hole No. 4	Skeletal remains of 1 individual	Guilday et al., 1964
		HISTORICAL RECORDS	
1821	McKean-Warren cos.	Author observed "sable skins" from trapline	Tome, 1928
1868	Clinton and Potter cos., headwaters of Young Woman's Cr.	5–6 trapped by Mr. Thomas	Rhoads, 1903; Shoemaker, 1929
1870	Potter Co.	Austin reports collecting individuals	Rhoads, 1903
1892	Columbia Co., mts. N of Benton	Mr. Coward presented a skin to Philadelphia Academy of Sciences; specimen, ANSP 1563	Rhoads, 1897, 1903
1894	Cameron Co., Shippen Twp.	M. M. Larrabee acquired several pelts	Rhoads, 1897, 1903
1894–1895	Potter Co., E fork Sinnemahoning R.	M. M. Larrabee acquired 22 pelts	Rhoads, 1897, 1903
1895	Cameron Co., Shippen Twp.	M. M. Larrabee acquired 3 pelts	Rhoads, 1897, 1903
1895	Clinton Co., North Mt.	2 trapped by "Ock" Huff	Shoemaker, 1929
1895	Clinton Co., Rockey Place, head of Rockey's Run	1 killed according to J. Q. Dyce	Shoemaker, 1929
1895–1896	Sullivan Co., near Eaglesmere	R. W. Bennett reported 1 trapped	Rhoads, 1897, 1903
1899	McKean Co., Haven's Brook, Norwich Twp.	6 caught by T. Mulkins	Rhoads, 1903
1901	Sullivan Co.	1 male and 1 female caught by Behr; male given to Philadelphia Academy of Sciences; preserved specimen, ANSP 6303	Rhoads, 1903
1956	Potter Co., near Oswago	B. Bailey reported sighting one individual crossing the road	Bailey, 1957

Table 5.—*Continued.*

Date	Locality	Comments	References
	SPECIMEN RECORDS		
1892	Columbia Co., mts. N of Benton	Skin	ANSP 1563; Philadelphia Academy of Sciences
1901	Sullivan Co., Lopez		ANSP 6303; Philadelphia Academy of Sciences
1957	Wayne Co., South Sterling	Skin	Reading Public Museum and Art Gallery
1963	Wayne Co., Newfoundland, Dreher Twp.	Skeleton	CM 40436; Carnegie Museum Natural History
1970	Mercer Co., Bobby Run Cr., Hickory Twp.	Skull; collected by J. Lucas	CM 59587; Carnegie Museum of Natural History

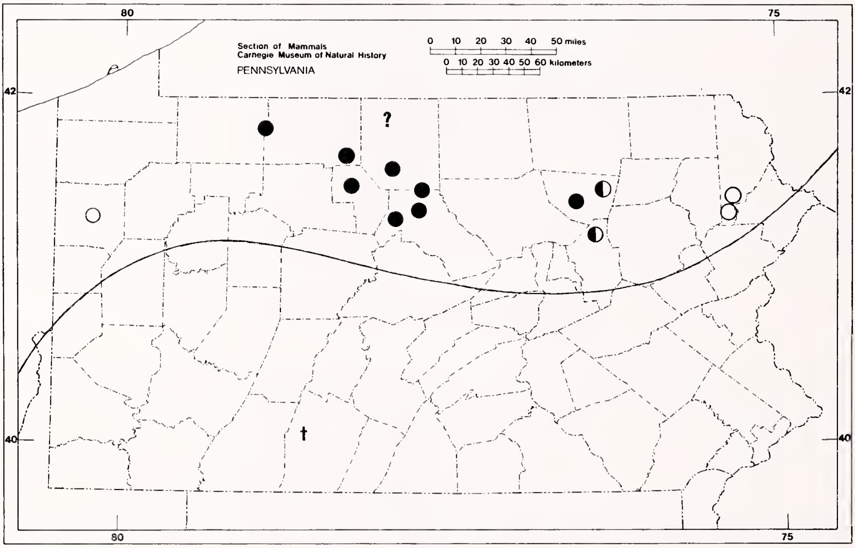
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Fig. 5.—Map of Pennsylvania showing location of records and possible distribution of *Martes americana* before it was extirpated. Specimens from Mercer and Wayne counties represent records since 1957. Symbols used are described in Fig. 1.

1964). The agility and arboreal nature of the species may have allowed it to escape from natural traps such as sinkholes and caves. However, its absence from archaeological sites is not explained unless it was regarded by the Indians as an animal to be protected. This possibility has been proposed by some authors (Guilday, 1961*b*; Shoemaker, 1919).

The distribution of historical records of *M. americana* in Pennsylvania would suggest that it was restricted to the northern third of the Commonwealth, specifically in the regions of McKean, Cameron, Potter, and Clinton counties, and Columbia and Sullivan counties (Table 5; Fig. 5). Hall (1981) also indicates this distribution with an extension southwestward into Ohio. The occurrence of the marten in Ohio is substantiated by specimens in the Cleveland Museum of Natural History (Bole and Moulthrop, 1942; Gottschang, 1981). Based on Pennsylvania records and comments by Hagmeier (1956), a southern extension of the distribution, at least in historical times, is questionable. However, such a distribution has been indicated by Bailey (1946) and Paradiso (1969).

The marten typically inhabits northern coniferous forests (Hagmeier, 1956). However, excessive trapping and clearing of forests caused the species to be extirpated in many areas (Allen, 1942). Because of the restricted geographical distribution of records of *M. americana* in Pennsylvania, it is difficult to determine any trends as the populations disappeared. It is likely the distribution receded in a northerly direction starting in Ohio. The marten was reported in 1838 as far south and west as Ross County, Ohio. Bole and Moulthrop (1942) reported two specimens from Ashtabula County and suggested the species was extirpated in Ohio before 1850. The earliest record in Pennsylvania was in 1821 from the vicinity of McKean and Warren counties. The last record for this time period in Pennsylvania was a specimen collected in 1901 from Sullivan County. The population receded into New York (Hagmeier, 1956).

Based on records since 1956 (see Table 5), it appears that *M. americana* may eventually become re-established in Pennsylvania. A sight record in Potter County (Bailey, 1957) and specimens from Wayne County suggest individuals are crossing over from New York. The presence of one specimen unexpectedly collected from Mercer County, Pennsylvania, in 1970 is difficult to explain.

***Martes pennanti*—fisher**

Martes pennanti has been called fisher, eastern fisher, pekan, fisher marten, Pennant's marten, tree otter, tree fox, black cat, black fox, fisher cat, and fisher weasel (Cunningham, 1985*b*; Powell, 1981, 1982; Seton, 1929*b*). This variety of names suggests that the secretiveness and scarcity of this species caused some confusion in identification. The fisher is dark brown to gray in color with blackish rump and hind legs. The tail is black. The total length of males and females is 990–1033 mm and 830–900 mm, respectively; the length of tail is 381–422 mm and 340–380 mm, respectively (Hall, 1981).

The distribution of *M. pennanti* in the eastern United States extended as far south as the forested areas of North Carolina and Tennessee (Powell, 1982). Remains of the fisher occasionally show up in paleontological and archeological sites in Pennsylvania (Table 6). The oldest records are from Bedford (Guilday et al., 1964) and Washington counties (Guilday et al., 1980), which date back about 11,000 years. Skeletal remains from archaeological sites have been recorded up to historic times (Guilday et al., 1962). Early historic records make reference to this species existing in Pennsylvania, but the relatively small size of the fisher probably did not warrant extensive documentation of specific encounters. The first record of a captured individual from Pennsylvania is the classical account of one collected by Spencer F. Baird for illustration in James J. Audubon's *The Viviparous Quadrupeds of North America*. Many of the later accounts were verbal reports which were eventually compiled by individuals such as Rhoads (1903). The records of individuals captured or killed in Pennsylvania are relatively few; the number of known Pennsylvania specimens existing in museums is five. Although the last dates of individuals being taken are 1921 and 1923, there are other reports of later sightings of individuals or tracks (Cunningham, 1985*b*; Hamilton, 1943; Poole, 1932).

Before colonial times the fisher may have occurred in most parts of Pennsylvania with the possible exception of the southeast counties of Northampton, Lehigh, Bucks, Montgomery, Chester, Delaware, and Philadelphia (Fig. 6). Although the fisher may have also been absent in northwestern Pennsylvania as well, its presence is suggested by records from Ashtabula County, Ohio, in 1837 (Bole and Moulthrop, 1942). Also, Guilday (1956) reports an archaeological record west of Pennsylvania in Hancock County, West Virginia. The extirpation of *M. pennanti* in most areas was caused by extensive trapping and clearing of forested areas. Based on historical records it appears that during colonial times the distribution of *M. pennanti* in Pennsylvania had receded from the southwestern regions. Eventually the activities of man caused the distribution of the fisher to recede northward into New York with population densities being very low (Powell, 1982).

Martes pennanti may become re-established in Pennsylvania sometime in the future as a result of stocking programs in adjacent states. In New York, individuals were transferred from the existing natural population in the Adirondacks to the Catskill Mountains (Powell, 1982).

Table 6.—*Paleo-archaeological, historical, and specimen records of* Martes pennanti *from Pennsylvania.*

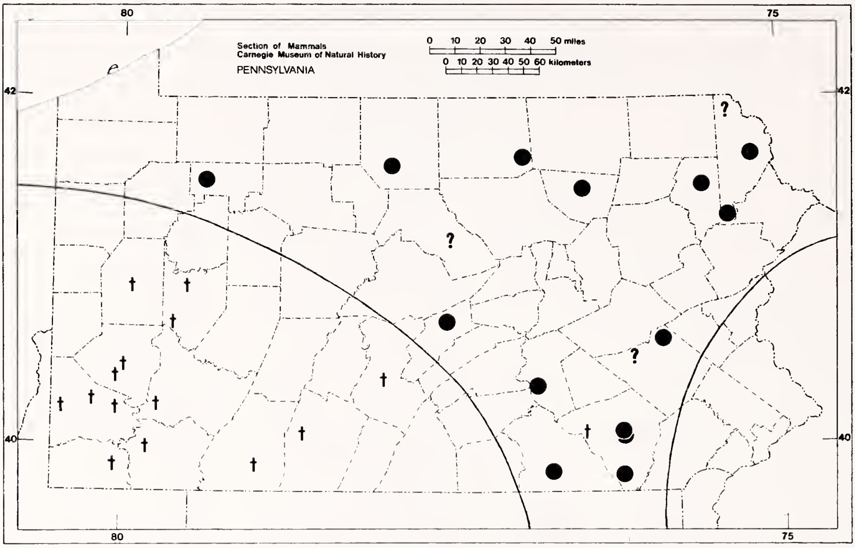
Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
N.D.	Armstrong Co., Mahoning Twp., Wadding Rockshelter (36Ar21)	Skeletal remains	Guilday et al., 1980
N.D.	Armstrong Co., South Buffalo Twp., Murphy's Old House Site (36Ar129)	Skeletal remains	Guilday et al., 1980
N.D.	Greene Co. Cumberland Twp., Hartley Site (36Gr23)	Skeletal remains	Guilday et al., 1980
N.D.	Washington Co., North Strabane Twp., Boyle Site (36Wh19)	Skeletal remains	Guilday et al., 1980
N.D.	Washington Co., Union Twp., Mathies Mine Village Site (36Wh54)	Skeletal remains	Guilday et al., 1980
N.D.	Westmoreland Co., Sewickley Twp., Janitor Site (36Wm21)	Skeletal remains	Guilday et al., 1980
11,300 ± 700 BP	Washington Co., Jefferson Twp., Meadowcroft Rockshelter (36Wh297)	Skeletal parts representing 1 individual	Guilday et al., 1980
11,300 ± 1000 BP	Bedford Co., near New Paris, Sink Hole No. 4	1 first upper molar at 6.1 m depth	Guilday et al., 1964
920–1190 AD	Somerset Co. Summit Twp., Gnagey Site, (36So55)	1 skeletal part representing 1 individual	George, 1983
1100 AD	Allegheny Co., Collier Twp., Drew Site (36Al62)	2 skeletal parts representing 1 individual	Buker, 1970; Guilday et al., 1980
1390 ± 105 AD	Butler Co. Summit Twp., Bonne Brook Site (36Bt43)	1 skeletal part representing 1 individual	Guilday et al., 1980; Herbstritt, 1981
1330 AD	Allegheny Co., Stowe Twp., McKees Rocks Village Site (36Al16)	2 skeletal parts representing 1 individual	Guilday et al., 1980; Lang, 1968
1400–1525 AD	Fayette Co. Redstone Twp., Campbell Site (36Fa26)	Skeletal remains	Guilday et al., 1980

Table 6.—*Continued.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
1600–1625 AD	Lancaster Co., 2 mi S Columbia, Washington Boro, Eschelman Site (36La12)	3 skeletal parts representing 2 individuals	Guilday et al., 1962
	HISTORIC RECORDS		
1844	Dauphin Co., 6 mi above Harrisburg	1 collected by S. F. Baird for J. J. Audubon	Doutt et al., 1973; Rhoads, 1903; Shoemaker, 1919, 1929
About 1853	Tioga Co., Ward Twp.	1 shot by Cleveland	Rhoads, 1903
1857	Wayne Co., Oregon Twp.	1 caught by L. N. Goodnough	Grimm and Whitebread, 1952; Rhoads, 1903
Pre-1865	Berks Co., the Pinnacle	2 killed by J. Saylor	Poole, 1932
1871	Lancaster Co., Martic Twp., near Drumore Line	1 captured by McCalf and examined by member of Linnean Society	Records of the Lancaster Linnean Society, 24 Feb 1872 (No. 294)
1874	Sullivan Co., Loyalsock Cr.	M. S. Prescott (=Trescott) reported 1 killed	Rhoads, 1903; Shoemaker, 1919; Warren, 1897*a*, 1897*b*
About 1876	Berks, Co., near Mountain	A. Kreitz treed 1 "tree otter"	Poole, 1932
About 1879	Wayne Co., headwaters of Butternut Cr.	1 caught by G. Stevens	Rhoads, 1903
1879	York Co., Codorus Twp., near the Texas mill	1 "black wild-cat" was killed by D. Hamm	Item, 28 Nov 1879; Harrisburg Daily Patriot, 5 Dec 1879
About 1885	Lackawanna Co., near Olyphant	2 killed by M. Crippen, one which was given to I. F. Everhart	Grimm and Whitebread, 1952; Rhoads, 1903; Warren, 1897*b*
About 1893	Forest Co., Allegheny R.	1 killed by J. Bush	Rhoads, 1903; Shoemaker, 1919
1894–1895	Potter Co., east fork of Sinnemahoning Cr.	22 pelts purchased from a hunter	Rhoads, 1903; Shoemaker, 1919
1895–1896	Cameron Co.	Shoemaker (1919) misquoted Rhoads (1903) by saying several were taken; in actuality several	Shoemaker, 1919

Table 6.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
		M. americana were obtained in 1894–1895	
1896	Lancaster Co., Mill Cr., 2 mi N Bird in Hand (3 mi E Lancaster)	1 killed by C. S. Nunnemacher and given to M. W. Raub of Lancaster	Allen, 1942; Doutt et al., 1973; Guilday et al., 1962; Hall, 1981; Poole, 1932; Rhoads, 1903; Shoemaker, 1919
1900	Clinton Co., near Mill Hall	Pfoutz reported 1 seen	Rhoads, 1903; Shoemaker, 1929
1921	Lancaster Co., 3 mi S Holtwood	H. J. Roddy (Franklin and Marshall (Museum) reported 1 captured	Hamilton, 1943; Poole, 1932
1923	Mifflin Co., Seven Mts., near Milroy	Central Pennsylvania newspaper report 1 "black cat" killed	Shoemaker, 1929
1931	Berks Co., Blue Ridge Mt. above Strausstown	S. Wishnieski and E. L. Poole found tracks and verified drawings with U.S. Biological Survey	Hamilton, 1943; Poole, 1932
1982	Wayne Co.	1 observed by R. E. Moase (Fisheries Technician)	Personal telegram to "C. N. Shiffer," 10 Nov 1982 (copy on file with map at Carnegie Museum of Natural History)
	SPECIMEN RECORDS		
Cataloged 1859	Locality unknown	Skin and skull	ANSP 507; Philadelphia Academy of Sciences
N.D.	Locality unknown	Skull only	ANSP 2130; Philadelphia Academy of Sciences
N.D.	Lancaster Co.	Body mount	Franklin and Marshall College
N.D.	Locality unknown	Body mount	Franklin and Marshall College
N.D.	Cumberland Co., Carlisle caves	Skeletal parts	USNM 1848; U.S. National Museum of Natural History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Carnegie Museum of Natural History
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Fig. 6.—Map of Pennsylvania showing location of records and possible distribution of *Martes pennanti* before it was extirpated. Question marks in Berks and Wayne counties represent possible occurrences in 1931 and 1982, respectively. Symbols used are described in Fig. 1.

It is possible that an individual recently seen in Wayne County, Pennsylvania (see Table 6), originated from the Catskill Mountains. In 1969, 23 individuals from New Hampshire were released in West Virginia (Powell, 1982). With these local introductions and the increased awareness for habitat and wildlife preservation, it is possible the fisher will become re-established in Pennsylvania.

***Taxidea taxus*—badger**

The natural occurrence of *Taxidea taxus* in Pennsylvania has been questioned (Kitchen, 1950; Warren, 1897). Many of the records of the badger have been disclaimed as individual introductions. However, there are some indications that this species has naturally occurred in Pennsylvania in the past, and perhaps in recent years. Catherman (1946) indicated that local people in Pennsylvania were uncertain about the characteristics of the badger. The badger has a flattened posture, grayish colored pelage, a distinctive white middorsal stripe from the snout to shoulders, brownish to black feet, and black preauricular and postauricular spots. Males have a total length and length of tail measuring 629–870 mm and 108–155 mm, respectively; females have corresponding measurements of 521–790 mm and 98–155 mm.

Table 7.—*Paleontological, historical, and specimen records of* Taxidea taxus *from Pennsylvania.*

Date	Locality	Comments	References
	PALEONTOLOGICAL RECORDS		
Pleistocene	Montgomery Co., on Schuylkill R., below Valley Forge, Port Kennedy Cave	Skeletal remains	Cope, 1871, 1889; Guilday et al., 1964; Hay, 1923; Rhoads, 1903
3722 ± 200 BP	York Co., Manchester Twp., ¼ mi E Emigsville, Bootlegger Sink	Skeletal remains of 2 specimens	A. McCrady, Section of Vertebrate Fossils, Carnegie Museum of Natural History, personal communication
	HISTORICAL RECORDS		
1892–1897	Locality unknown	1 captured; assumed to have escaped from captivity	Warren, 1897*b*
1946	Indiana Co.	1 killed by R. Olsen	Catherman, 1946; Genoways, 1985
1950	Fayette Co., Uniontown	Obtained by T. W. Meehan who transferred to Carnegie Museum of Natural History; preserved specimen, CM 61342	Genoways, 1985
1950	Washington Co., Cecil Twp.	1 captured	Kitchen, 1950
1955	Beaver Co., N of New Galilee	1 killed on road	McGregor, 1955
	SPECIMEN RECORDS		
1950	Fayette Co., Uniontown, Berkeley-Union Street	Skull	CM 61342; Carnegie Museum of Natural History

Paleontological records of *T. taxus* have come from Montgomery and York counties (Kurtén and Anderson, 1980; McCrady, personal communication). These records, and one from Cumberland Cave, Allegany County, Maryland (Gidley and Gazin, 1938), indicate *T. taxus* in the past inhabited at least the southeastern region, and possibly the southern portions of Pennsylvania.

There is one known record of the badger prior to 1900. Warren (1897*b*) reported one individual captured between 1892 and 1897 and assumed it to be an "escaped captive." The lack of additional records

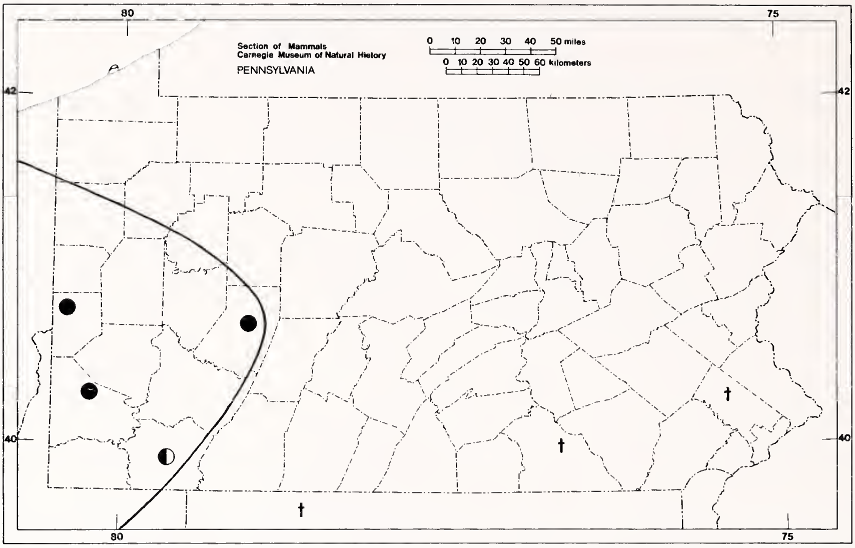
Section of Mammals
Carnegie Museum of Natural History
PENNSYLVANIA
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Fig. 7.—Map of Pennsylvania showing location of records and the possible distribution of *Taxidea taxus* since 1944. Symbols used are described in Fig. 1.

during that time period from adjacent areas supports this assumption. It is probable that the badger did not occur in Pennsylvania from colonial times through 1900.

Between 1946 and 1955, four badgers were reported (Table 7) from Pennsylvania, specifically from Beaver, Fayette, Indiana, and Washington counties (Fig. 7). It is possible that the species is extending its range eastward into Pennsylvania. This trend has already been noted in Ohio (Gottschang, 1981) with the easternmost record being Geauga County, Ohio (approximately 120 km from the Beaver County record in Pennsylvania). Genoways (1985) explains how the right-of-way along interstate highways may provide suitable habitat and could promote a natural dispersal of the badger from Ohio to Pennsylvania. If the badger is not actively extending its range eastward into Pennsylvania, then the only explanation for the occurrence of the species in the Commonwealth is importation of animals that subsequently escaped captivity or were released. Nugent and Choate (1970) have commented in such badger records from other parts of the northeastern United States.

Felis concolor—mountain lion

Felis concolor has been identified by various common names including panther, painter, cougar, mountain lion, puma, catamount, Indian devil, Alleghenian cougar, Adirondack cougar, American lion, Pennsylvania lion, brown tiger, bender (Pennsylvania Dutch), tiger tail, and long-tailed cat (Allen, 1942; Poole, 1932; Rhoads, 1903; Seton, 1929*a*; Shoemaker, 1929). Although its appearance is distinctive from other mammals occurring in the Commonwealth, the name "catamount" has been used for this species as well as both the bobcat and lynx. For this reason some confusion has emerged. Thus, all historical records referring to "catamounts" without further descriptive information have been omitted.

Originally, the mountain lion occurred from New England southward to Florida (Allen, 1942; Young and Goldman, 1946). Kurtén and Anderson (1980) describe its habitat as "eurytopic" but with preferences for "forest, especially in the mountains, and tall grass prairie." In Ohio, it has been considered extirpated since 1850 (Gottschang, 1981). Hamilton (1943) believes it was extirpated from the Adirondacks by 1903. McKeever (1954) felt that the decline of the mountain lion in West Virginia began by the mid-1800's. It was thought to be completely extirpated in that state by about 1900. Paradiso (1969) says the mountain lion was extirpated in Maryland by the end of the nineteenth century. In both Maryland and West Virginia sightings, tracks, and "screams" have been reported, but Paradiso (1969) and McKeever (1954) are unequivocal regarding the extirpated status of the species.

Paleontological and archaeological records of mountain lion in Pennsylvania are not common and are restricted to only three sites (Table 8; Fig. 8A). Guilday (1961*b*) suggests that this species held spiritual significance for the Indians. He felt this might explain its conspicuous absence from archaeological sites.

During the 18th and 19th centuries, the mountain lion was viewed with a great deal of fear by many inhabitants of the Commonwealth. Newspaper accounts fueled these fears by attributing attacks on man and domestic animals to this species. Thus, the killing of a mountain lion was a matter of pride that was remembered by many hunters for years after a small record had been placed in the local newspaper. Such accounts were popular and frequently were telegraphed to other newspapers in the Commonwealth. The bounty system, which was initiated throughout Pennsylvania in 1807, provided additional incentive for hunting mountain lions.

Man may have also affected the existence of the mountain lion in another way. The decline of this species in Pennsylvania may be linked to decimation of forest habitat and the accompanying decline of its primary prey species, the white-tailed deer (see white-tailed deer account).

Historical records show a concentration of mountain lions in north-central Pennsylvania and, to a lesser degree, in the Pocono Mountains

Table 8.—*Paleo-archaeological, historical, and specimen records of* Felis concolor *from Pennsylvania.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
Recent	Cumberland Co., Carlisle caves	Cave deposits	Miller, 1940
1330 AD	Allegheny Co., Stowe Twp., McKees Rocks Village Site (36Al16)	1 skeletal part representing 1 individual	Lang, 1968
1600–1625 AD	Lancaster Co., Washington Boro, 3 mi S Columbia, Eschelman Site (36La12)	5 skeletal parts representing 2 individuals	Guilday et al., 1962
	HISTORICAL RECORDS		
1729	Lancaster Co., Conestoga	1 killed	Watson, 1844
About 1729	York Co., Shrewsbury	1 killed by an Indian	Rhoads, 1903; Watson, 1844
1784	Centre Co.	1 killed by A. Boggs	Linn, 1883
About 1790	Luzerne Co., Capouse Mt.	1 killed by Wheaton	Pearse, 1866
1794–1808	Sullivan Co.	Bounty paid to Reeves, Youns, Rogers, and Bill	Ingham, 1899
1795	Lycoming Co., Pine Cr.	1 killed by Tome	Fergus, 1982
1797	Centre Co., Bald Eagle Mt.	1 killed by Pentz	Shoemaker, 1916, 1949
About 1798	Bradford Co.	1 killed by J. McKean, Jr. and P. DeWitt	Bradsby, 1891
1800–1805	Susquehanna Co.	5 killed by J. Sabin	Blackman, 1873
1805	Bradford Co., 120 mi radius of Wyoming Valley	72 killed by 600 hunters during June	Heverly, 1926
1808–1820	Luzerne Co.	Averaged 50 bounties/year	Harvey, 1927
1810	Greene Co., Dunkard Cr.	1 killed	Grimm and Roberts, 1950
1811	McKean Co. Sartwell Cr.	1 killed by M. S. Burt during the winter	Beebe, 1934
1811	Butler Co.	1 killed by T. Sampson on 15 Aug	Webb and Stevens, 1934
1812	Butler Co.	1 killed by J. McGinley on 12 Dec	Webb and Stevens, 1934
1813	Clearfield Co., Boggs Twp., Clearfield Cr.	1 killed by S. Turner	Aldrich, 1887
1814	Bradford Co.	Bounties paid on 1 Feb	Bradford Gazette, 1 Feb 1814; Bradsby, 1891

Table 8.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1815	Wyoming Co., Mehoopany Cr.	1 killed by R. and E. Robinson on 9 Dec	Columbian Chronicle, 6 Jan 1816
1818	Luzerne Co.	50 killed	Heverly, 1915
1822	Potter Co.	6 killed; bounties paid to J. Ayers, J. Pitcher, J. Vannetter, and 3 Indians	Leeson, 1890
1824	Centre Co., foot of Alleghenies	2 killed by J. Mitchell	Pennsylvania Intelligencer, repr. from Juniata Gazette and Franklin Repository, 28 Dec 1824
1824	Susquehanna Co., Jackson	1 killed by B. Samson and J. Lindsey on 22 Jan	The Pennsylvania, 14 Feb 1824; repr. from Montrose Gazette
1825	Centre Co., near Philipsburg	1 killed by Mitchell on 8 Dec	Reading Chronicle, 12 June 1832
1826	McKean Co.	Bounties paid to S. Cole, B. Freeman and Junmerson	Leeson, 1890
1827	McKean Co.	Bounties paid to J. Silverkeel, D. Killbuck, S. Beckwith, W. Lewis, D. Lewis, R. Hill	Leeson, 1890
1827	Northampton Co., 17 mi from Easton	1 killed during Feb	Watson, 1844; Rhoads, 1903
1828	Northampton Co., Pocono Mts.	3 killed by J. Vliet	Harrisburg Argus, 29 Mar 1828; repr. from Easton Argus; Hazard, 1828
1828	Centre Co.	P. Cambridge attacked during Feb	Harrisburg Chronicle, 25 Feb 1828; repr. from Centre Democrat
1829	Washington Co., West Bethlehem Twp.	1 killed by A. Rickelt on 1 Dec	Forrest, 1926
1829	McKean Co.	Bounty paid to P. Reed	Leeson, 1890
1830	Clinton Co., Sugar Valley	1 killed by H. Barner	Linn, 1883
1830	Franklin Co., Loudon	1 killed in Nov	Franklin Repository, 23 Nov 1830; repr. from Franklin Republican;

Table 8.—*Continued.*

Date	Locality	Comments	References
		Historical Records	
			Allegheny Democrat and Farmers and Mechanics Advertiser, 30 Nov 1830; Hazard, 1830*b*
1830	Lackawanna Co., Covington Twp.	1 killed by D. Scott	Allegheny Democrat and Farmers and Mechanics Advertiser, 11 May 1930; repr. from Wilkes-Barre Democrat; National Gazette and Literary Register, 27 April 1830
1830	Mifflin Co., Armagh Twp.	1 killed in Oct	U.S. Gazette, 2 Nov 1830
1830	Northampton Co., West Bethlehem	1 killed, 1 escaped	Hazard, 1830*a*
1832	Bedford Co., Allegheny Mts., near Bedford	1 killed in Feb	U.S. Gazette, 15 Feb 1832
1833	Elk Co., Boone Mt.	3 killed by J. and P. Vasbinder	McKnight, 1898, 1905*b*; Rhoads, 1903
1833	Elk Co., Medix Run	5 killed by J. Long	McKnight, 1905*a*
1833	Elk Co., Medix Run	6 killed by P. Smith and E. Morey in March	McKnight, 1905*a*
1833–1840	Clearfield Co., near Coalsport	1 killed by A. Nevling, skin now owned by grandson	The Daily J., 20 July 1965
1834	Lehigh Co., Lehigh Gap	2 killed	Pennsylvania Reporter, 7 Jan 1934; Union Times and Republican Herald, 10 Jan 1834; repr. from Miners Journal
1835	Northampton Co.	5 killed by J. Eschenbach, B. F. Berry on 18 Feb	Pennsylvania Reporter and Democratic Herald, 13 Mar 1835
1840	Tioga Co., Liberty Twp.	Cleveland reported 1 killed by J. and J. Seachrist	Rhoads, 1903

Table 8.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1841	Potter Co.	Austin reported 1 killed by H. Hurlburt	Rhoads, 1903
1846	Venango Co., Franklin	1 killed	Pennsylvania Telegraph, 19 Aug 1846
1847	Potter Co.	Bounties paid	Beebe, 1934
1848	Forest Co.	Last bounty paid	Walker, 1960*b*
1850	Bradford Co., Marcy Run	1 killed by J. Crammer	Heverly, 1885
1850	Fayette Co., Dunbar's Camp	1 killed	Grimm and Roberts, 1950
1851	Cameron Co., between Stirling and Driftwood, on the Driftwood	Dickerson reported 2 killed by I. Rammage	Rhoads, 1903
1851	Cameron Co.	Last bounty paid	Walker, 1960*b*
1853	Elk Co.	6 killed	Luzerne Union, 11 May 1853
1854	Mifflin Co. Seven Mts., near Milroy	Rothrock reported 1 killed	Rhoads, 1903
1855	Jefferson Co., Sandy Lick	5 killed	True Democrat, 25 Jan 1855
1855	Clearfield Co.	1 killed by M. Long	True Democrat, 12 July 1855; repr. from Clearfield Republican
1856	Susquehanna Co., Susquehanna	Friant reported 1 killed by S. E. Brush reported to be last killed in Commonwealth; preserved specimen, PSU 1-14562	Rhoads, 1903; Walker, 1960*b*
1857	Elk Co.	Last bounty paid	Walker, 1960*b*
1858	Clinton Co.	1 killed by S. Snyder	True Democrat, 28 Jan 1858
1858	Bradford Co., Albany Twp.	Cleveland reported 1 killed by P. Wilcox during winter	Rhoads, 1903
1858–1859	McKean Co.	1 killed by Eastman and S. Dickeson	Rhoads, 1903
1859	McKean Co.	Last bounty paid	Walker, 1960*b*
1859	Indiana Co., Armstrong Twp.	C. Beatty attacked	Patriot and Union, 11 Oct 1839
1860	Clinton Co. Young Woman's Cr.	1 killed by J. Snyder	Walker, 1960*b*
1861	Somerset Co., Allegheny Mts.	1 killed by J. Hostetler	Grimm and Roberts, 1950

Table 8.—*Continued.*

Date	Locality	Comments	References
HISTORICAL RECORDS			
1863	Cambria Co., Conemaugh Valley	1 killed	Grimm and Roberts, 1950
1863	Warren Co.	1 killed	Walker, 1960*b*
1864	Tioga Co., Ward near Fallbrook	1 seen by W. R. Lyon, reported by Cleveland	Rhoads, 1903
1866	Pike Co.	3 killed	Patriot Daily Union, 30 Oct 1866
1866	Centre Co., near Unionville	1 killed	Patriot Daily Union, 10 Nov 1866
1866	Centre Co.	1 killed	Patriot Daily Union, 10 Nov 1866
1867	Centre Co.	3 escaped, 8 killed by two parties during Jan	Patriot and Daily Union, 7 Jan 1867
1867	Wayne Co.	1 killed by T. Anson	Shoemaker, 1948*a*
1867	Clearfield Co., near Indiana Co. line	1 killed by H. Kelly during Dec	Greensberg Herald, 30 Dec 1867
1869	Clearfield Co.	1 killed by Kelly and Zayer	True Democrat, 20 Jan 1869
1870	Centre Co.	1 killed by W. Perry	Shoemaker, 1949
1870	Jefferson Co. within 50 mi of Reynoldsville	Reported to be last killed in region	Elliott, 1894
1871	Clinton Co.	2 killed (may be same as next report)	Daily Patriot, 10 Jan 1871
1871	Clinton Co., Big Run at Beech Cr.	2 killed by J. David and G. Hastings	Altoona Tribune, 20 Feb 1941; Linn, 1883; Rhoads, 1903
1872	Jefferson or Clearfield Co.	1 killed by J. Long	McKnight, 1905*a*
1873	Blair Co., near Newry	1 killed; reported to be last killed in county by S. Boos	Altoona Tribune, 20 Feb 1941
1873	Centre Co.	1 wounded by J. Switzer	True Democrat, 18 Dec 1873
1873	Pike Co.	2 seen during Oct	Anon., 1873; Rhoads, 1903
1873	Snyder Co. Centerville, Jacks Mt.	1 killed by F. Boyer	Shoemaker, 1948*a*
1874	Susquehanna Co., near Clifford	1 killed by S. Odin	Gifford and Whitebread, 1952; Rhoads, 1903;

Table 8.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
			Shoemaker, 1948*a*
1874	Berks Co., north end Albany Twp., Blue Mts.	1 killed by T. Anson in August	Anon., 1874; Poole, 1932; Rhoads, 1903; Shoemaker, 1948*a*
1875	Cambria Co., Stony Cr., 12 mi from Johnstown	Shields reported 1 killed	Rhoads, 1903
1875	Clinton Co. Spruce Run	1 killed by J. Roan	Walker, 1960*b*
About 1876	Northeastern Pennsylvania	Mrs. B. H. Warren reported 1 killed	Young, 1954
1876	Centre Co., Yost Run	1 killed by J. Perry	Walker, 1960*b*
1876	Tioga Co., Clymer	1 killed and photographed by B. Jaquin	Corry Evening J., 12 Sept 1946
1877	Bedford Co., East Providence Twp.	1 killed	The Globe, 23 Jan 1877; repr. from Bedford Inquirer
1879	Snyder Co., Duncan Mills	1 killed by J. and E. Daton, and H. Warren, may be same as 1876 record from Mrs. Warren	Snyder County Tribune, 19 June 1879
1880	Blair Co.	1 killed by S. Boone	Item, Glen Rock, 9 Jan 1880; Huntingdon Journal, 9 Jan 1880
1880	Clearfield Co., Mosquito Cr.	2 killed by C. F. Herlacher during Feb	Shoemaker, 1948*a*
1880	Westmoreland Co.	1 shot by a pair of hunters	Tribune Herald, Greensburg, 21 Dec 1880
1881	McKean Co., Hamilton Twp.	1 killed by L. Palmiter during July	Harrisburg Daily Patriot, 27 Jul 1881
1822	Centre Co., Rock Run	3 killed by A. Hall	Shoemaker, 1943
1886	Centre Co., foot of Rattlesnake Mtn.	Bounty paid to J. Lucas	Shoemaker, 1943; Walker, 1960*b*; Daily J., 20 July 1965
1886	Centre Co.	Bounty paid; could be same as previous record	Rhoads, 1903; Warren, 1897*b*
1887	Washington Co., McClelland's Bridge	1 killed by J. Iams	Grimm and Roberts, 1950

Table 8.—*Continued.*

Date	Locality	Comments	References
	Historical Records		
1891	Clearfield Co.	2 killed by S. Nelson and the Askeys	Goodwin, 1936; Warren, 1897*b*
1892	Mifflin Co. Treaster Valley	4 cubs removed from den by C. Herlacher	Shoemaker, 1948*a*
1892	Venango Co., Sandy Cr.	1 killed by A. Carr during Feb	Titusville Herald, 22 Dec 1967
1893	Centre Co.	1 killed by J. Moore	Rhoads, 1903
1893	Clinton Co., Big Run at Beech Cr.	1 killed by the Longs	Warren, 1897*b*
1893	Mifflin Co., Treaster Valley	2 cubs killed by C. Herlacher	Shoemaker, 1916, 1948*a*
After 1896	Clinton Co., Tangascootac	1 killed by J. Simcox	Altoona Tribune, 20 Feb 1941
1898	Elk Co. Johnsonburg	1 hit by train; witnessed by M. Sullivan	Walker, 1960*b*
1900	Clinton Co., Eagleton	Unconfirmed sighting	Seton, 1929*a*
1901	Tioga Co., Brookfield	1 caught in trap and shot; witnessed by D. Reynolds	Walker, 1960*b*
1902	[Clinton Co., Tangascootac]; Simcox Lumber Company, on Scootac	1 killed	Walker, 1960*b*
1903	[Clinton Co., Tangascootac], on Scootac	1 killed by E. Monaghan	Walker, 1960*b*
About 1904	Blair Co., about 3 mi W Altoona	Unconfirmed sighting	White, 1956
About 1905	Blair Co., Canoe Cr., near Williamsburg	Unconfirmed sighting	White, 1956
1906	Clearfield Co., LeContes Mills, around Deer Cr. and Little Deer Cr.	Unconfirmed sighting	Smith, 1960
1914	[Union Co.], Paddy Mt.	1 killed by deer hunters	Shoemaker, 1943; taken from report in Lewisburg Journal, n.d.
1914	Centre Co., Rock Run	3 cubs killed by A. Hall	Walker, 1960*b*
1916	Blair-Cambria Co. line, at head of Bob's Cr.	1 observed by R. B. Long's woodcutters	Shoemaker, 1943
1923	Clinton Co., Kettle Cr., near Renovo	Unconfirmed sighting	Smith, 1960; Walker, 1960*b*
1940 or 1941	Potter Co., near Costello	Several unconfirmed sightings	Grove, 1956
1949	Indiana Co., between	Several unconfirmed	Zaycosky, 1949

Table 8.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
	Indiana and Canoe twps.	sightings reported to Game Protector	
1950	Venango Co., west of Sandy Cr., Hell's Kitchen area	1 sighted by A. Sopher and C. Irwin	Titusville Herald, 22 Dec 1967
1952	Lycoming Co., Cummings Twp., on Peterbaugh Mt., about 6 mi from Waterville	"Black panther" wounded and escaped; unconfirmed sighting	Weaver, 1956
1954	Blair Co.	Unconfirmed sighting and tracks during spring 1954	DeClaire, 1956
1960	Clarion Co., near Shippenville	1 sighted by E. Bish on 1 Sept	personal communication to J. K. Doutt, 8 Nov 1969; Section files, Carnegie Museum of Natural History
1964	northern Crawford Co.	1 seen several times by A. Bennett	Titusville Herald, 22 Dec 1967
1965	Cambria Co., Glasgow	1 sighted by C. Kuhn during Oct	personal communication to J. K. Doutt, 13 Nov 1967; Section files, Carnegie Museum of Natural History
1967	Crawford Co., Venango Twp. near Edinboro	1 killed by J. Gallant probably a captive animal; preserved specimen, CM 59525; 2 sighted at time of kill on 28 Oct	Anon., 1968*a*; McGinnis, 1982; Titusville Herald, 22 Dec 1967
1967	Crawford Co., Venango Twp.	Second cougar wounded by nephew of J. Gallant on 29 Oct	Titusville Herald, 22 Dec 1967
1967	Crawford Co., Sturgis Corner, 6 mi W Union City	1 wounded but not taken on 2 Dec	Titusville Herald, 22 Dec 1967
1967	Crawford Co.	1 wounded but never found by A. Bennett on 2 Dec	Titusville Herald, 22 Dec 1967
About 1969	Venango Co., Franklin	1 sighted by 3 separate people	Erie Times News, 2 Feb 1969

Table 8.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1969	Warren Co., Henry Mills	1 sighted in Jan	Erie Times News, 2 Feb 1969
1969	Tioga Co., Gaines	1 sighted several times during Sept and Oct	personal communication to J. K. Doutt by R. K. Wilson, 11 Dec 1969; Section files, Carnegie Museum of Natural History
1970	Allegheny Co., Sewickly Hts.	1 sighted by C. T. Marshall on 14 Nov	personal communication to J. K. Doutt, 17 Nov 1970; Section files, Carnegie Museum of Natural History
1970	Allegheny Co., Sewickley	1 sighted by C. J. Ramsburg on 30 Dec 1970, 6 Feb and 9 June 1971	personal communication to J. K. Doutt, 9 June 1971; Section files, Carnegie Museum of Natural History
		SPECIMEN RECORDS	
1847	Elk Co., Jay Twp., Wolflick Run	Skull	USNM 260574; U.S. National Museum of Natural History
1856	Susquehanna Co., Susquehanna	Body mount with skull enclosed	PSU 1-14562; Pennsylvania State University
1967	Crawford Co., Venango Twp., near Edinboro	Skull and partial skeleton; collected by J. Gallant	CM 59525; Carnegie Museum of Natural History

area (Table 8; Fig. 8A). The last known mountain lion to be killed from the northeastern region of the Commonwealth was taken in Susquehanna County in 1874. However, sightings, tracks, and reported kills have persisted in northcentral Pennsylvania throughout the current century. This agrees with Rhoads' (1903) comments regarding the heavy concentration of the species in the Allegheny Mountains. There was also a proliferation of sightings in western counties during the late 1960's and early 1970's. This may be explained by a report (Titusville

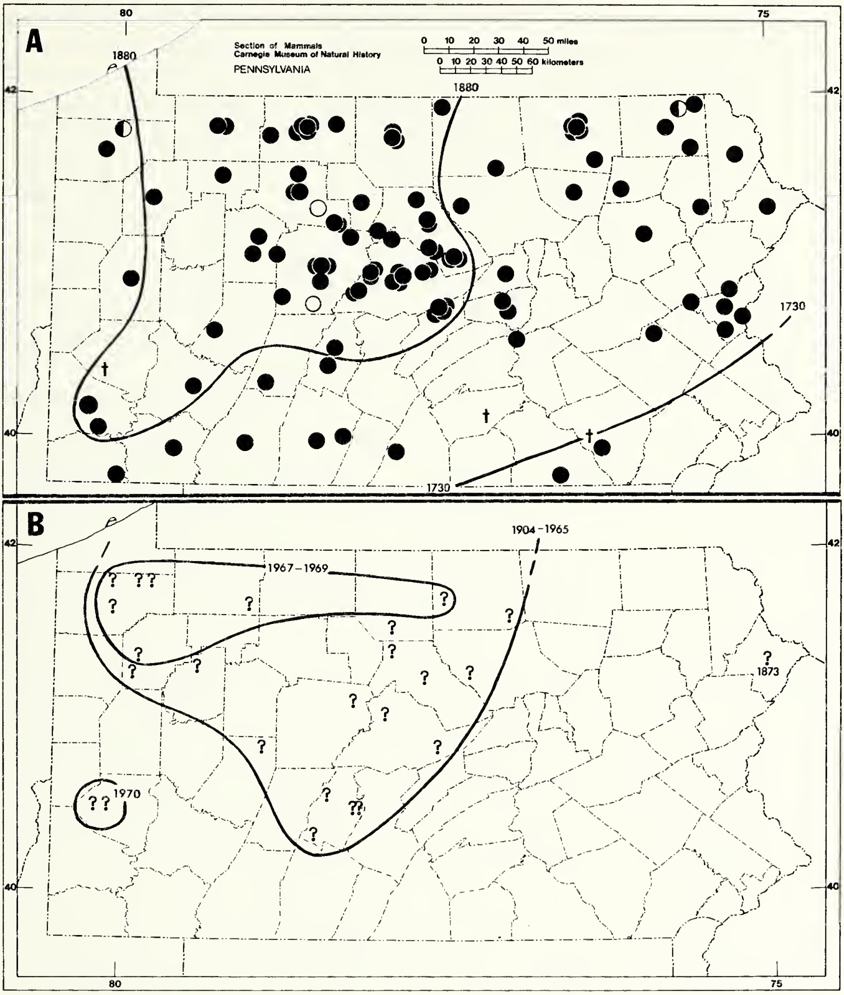

Fig. 8.—Map of Pennsylvania showing location of records of *Felis concolor*. (A) Archaeological, paleontological, and historical records of individuals known to have been collected in the Commonwealth since 1700. (B) Sightings which have occurred since 1873 (date of the last confirmed record according to Rhoads, 1903). Symbols used are described in Fig. 1.

Herald, 22 December 1967) that six captive mountain lions may have been released at a nearby Ohio locality.

The 1856 Susquehanna County specimen (Table 8) was preserved as a body mount with skull inside and is the property of The Pennsylvania State University. Perhaps because of its preservation and exhibition, it was long touted as the last mountain lion killed in Pennsylvania (Montrose Independent, 24 February 1966). Contrary to this information, nearly fifty animals were reported to have been killed or seen after that date (personal communications to J. K. Doutt; Rhoads, 1903; Shoemaker, 1929; Walker, 1960*b*). Rhoads (1903) could substantiate no reports after 1871; thus that date has been used as an arbitrary starting date for the recording of unconfirmed sightings in this paper (Fig. 8B). However, Shoemaker (1929) cited with confidence kills in 1892 and 1893. Records dating after Rhoads were discussed by Walker (1960*b*) and included mountain lions killed through 1914. In the early 1950's, several sightings of a black panther were reported in Cogan House Township, Lycoming County. Beginning about 1953, the sportsman's club in the area sponsored an annual event which was dubbed "the critter hunt." In 1954, a turn-out of 700 hunters concentrated on Bobst Mountain, about 20 miles northwest of Williamsport in an effort to collect this black panther (Wright, 1972). The local terminology of "critter" when making reference to sightings and events involving this particular sleek, black animal seems to indicate a reluctance to say specifically what the animal might be. Its identity has become more mysterious as a result of years of unsuccessful hunting by hundreds of people.

The Clearfield County specimen, preserved as a tanned skin owned by Nevling, and the Elk County skull housed at the U.S. National Museum of Natural History (Table 8) are, no doubt, authentic individuals native to the Commonwealth. However, the Crawford County specimen collected in 1967 has been examined and is thought by several individuals (Handley, personal communication; McGinnis, 1982) to be an escapee from a game park in Ohio. This individual is thought to represent a subspecies of the size native to Central America, not an immature specimen native to the Commonwealth. A larger mountain lion was reported to have been seen with this specimen at the time it was shot (McGinnis, 1982; Titusville Herald, 22 December 1967).

It is not known whether recent sightings and tracks represent similar escapees because no other mountain lions have been collected or photographed. However, the frequency of reported mountain lion sightings in Pennsylvania prevents an unequivocal decision on the status of *Felis concolor*. Isolated reports have been viewed by some with skepticism, but when such occurrences are grouped and plotted, a pattern of activity may emerge (Fig. 8B).

***Lynx canadensis*—lynx**

Lynx canadensis has been referred to by numerous common names. From the French name "loup cervier" which means "deer wolf," it was corrupted to "luci vee" and later "lucifer." The latter name made reference to the long black tufts of hair on the ears which were visualized by some as horns of the devil (Shoemaker, 1929). Other names include link, east Canadian lynx, catamount, gray wild cat, and lynx (Dalby, 1985; Rhoads, 1903; Seton, 1929*a*; Shoemaker, 1929).

The lynx has always been considered rare in Pennsylvania (Rhoads, 1903). This is substantiated by the scarcity of *Lynx canadensis* remains at paleontological and archaeological sites (Table 9). Although the remains of a *Lynx* species comparable to the size of the bobcat are not uncommon at paleo-archaeological sites, *L. canadensis* has only been positively identified at Hartman Cave, Monroe County. It has not been identified among the past or present faunas of Virginia (Bailey, 1946), Ohio (Bole and Moulthrop, 1942; Gottschang, 1981), Maryland (Paradiso, 1969), West Virginia (McKeever, 1954), or New Jersey (Rhoads, 1903). More than a century ago DeKay (1842) declared that the lynx was "not uncommon" in northern New York. Today, vagrants are infrequently taken in New York (Dalby, 1985). Godin (1977) states that viable populations exist in New England.

The physical similarities between *Lynx canadensis* and *L. rufus* have led to a great deal of confusion in identification. Historical accounts took particular care to make the distinction when the existence of more than one cat species of similar appearance was recognized. Descriptions placed careful emphasis on color, size, and weight of an individual that had been sighted or collected. Unfortunately, both species are approximately the same size, and the best method of recognizing the lynx is by looking for a short tail ringed with black-brown fur (Doutt et al., 1973; Fountain, 1976; Seton, 1929*a*). Most other external traits are relative in nature and might be difficult to interpret accurately without comparative material being present. As stated by Poole (1932), familiarity with the native fauna was not common among farmers or even sportsmen during early historical times.

Historical records (Table 9) reveal 25 accounts of *Lynx canadensis* being killed in the Commonwealth between 1834 and 1903. Fifteen of these accounts were followed up by Rhoads (1903), who apparently considers them credible. Warren (1897*b*) spent five years of inquiry on the question of *L. canadensis* in Pennsylvania. Although he felt he was unable to discover a single true example of the species personally, he believed there were two or three authenticated instances of lynx in the Commonwealth during the last quarter of the nineteenth century.

Typical habitat for this species is unbroken, mature boreal forests (Seton, 1929*a*; Godin, 1977). Nineteen of the 30 historical records of *L. canadensis* are from localities in the northern counties of the Commonwealth where such habitat existed. The other 11 records come from the southern tier of counties (Fig. 9). Eight of these lynx were

Table 9.—*Paleontological, historical, and specimen records of* Lynx canadensis *from Pennsylvania.*

Date	Locality	Comments	References
	PALEONTOLOGICAL RECORD		
Quaternary	Monroe Co. 2½ mi SW Stroudsburg, Hartman Cave (=Crystal Hill Cave)	5 skeletal parts	Leidy, 1889; Rhoads, 1903
	HISTORICAL RECORDS		
1790	Allegheny Co.	1 killed by Baum	Grimm and Roberts, 1950
1792	Greene Co., Dunkard Cr.	1 killed by J. Bobbett	Grimm and Roberts, 1950
1832	Philadelphia Co., vicinity Germantown	1 killed by E. Rittenhouse during winter	Watson, 1844
1834	Lycoming, Sullivan, and Tioga counties, between Loyalsock and Pine Cr.	3–4 killed by H. D. Moore	Rhoads, 1903
1842–1843	McKean Co., Norwich Twp., W branch Potato Cr.	1 killed by E. Dickinson	Rhoads, 1903
1849	Columbia Co.	1 killed by Buckalew	Grimm and Whitebread, 1952; Rhoads, 1903
1851–1852	McKean Co., Norwich Twp., W branch Potato Cr.	1 killed by E. Dickinson	Rhoads, 1903
1859	Lancaster Co., Martic Twp.	1 killed in Dec.	Lebanon Advertiser, 7 Dec 1859
1867	McKean Co., Kinzua Cr.	1 killed by T. J. Fenton	Rhoads, 1903
1867	McKean Co.	1 killed by E. Dickinson; reported to be last killed in county	Rhoads, 1903
1867	Locality unknown	1 killed by A. Parmeter	Rhoads, 1903
1868	Somerset Co., Negro Mt.	1 killed	Grimm and Roberts, 1950
1870	Cambria Co., near Cherry Tree	1 killed by W. S. Long	Grimm and Roberts, 1950
1871–1876	Sullivan Co., near Lopez	1 killed	Rhoads, 1903
1872–1874	Franklin Co., Kitatinny Mt.	6 killed by E. Straw	Harrisburg Evening Mercury, 24 Mar 1874
1874	Clinton Co., Hyner	1 killed by J. Pluff	Shoemaker, 1929
1875	Indiana Co., Banks Twp.	1 killed by J. E. Smith	Grimm and Roberts, 1950

Table 9.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1877	Fayette Co., Laurel Hill Mt.	1 killed	Grimm and Roberts, 1950
1880–1896	Potter or Cameron cos.	1 killed by Larrabee	Rhoads, 1903
1881	Lackawanna Co., Spring Brook Twp.	1 killed by J. Weaver	Grimm and Roberts, 1950; Rhoads, 1903
After 1881	Lackawanna Co., Lehigh R., Ash Gap	1 killed by C. Donnelly	Rhoads, 1903
1892–1899	Wayne Co., (northern part)	1 killed	Rhoads, 1903
1896	Lycoming Co., Roaring Branch	1 killed	Rhoads, 1903
1898	Westmoreland Co., Ligonier Twp., Laurel Hill Mt.	1 killed by L. T. Wiemer	Grimm and Roberts, 1950
Pre-1900	Somerset Co., 2137 ft.	1 trapped and tanned by D. C. Barclay	Rhoads, 1903
1900	Potter Co.	Austin reports occasionally paying bounties	Rhoads, 1903
Pre-1901	Tioga Co., Ward Twp., Tioga R.	1 killed by Cleveland	Rhoads, 1903
1903	Clinton Co., at head of McElhattan Run	1 killed by S. Motter	Shoemaker, 1929
1926	Monroe Co., Pocono Lake	1 killed by H. Slutter	Grimm and Whitebread, 1952
1926	Monroe Co., between Brady's Lake and Pocono Lake on Tobyhanna Rd.	1 killed by H. Slutter	Grimm and Whitebread, 1952
	SPECIMEN RECORDS		
1923	Tioga Co., near Antrium	Skin	Reading Public Museum and Art Gallery (unnumbered specimen)

collected in the southwestern corner of the Commonwealth during the last 30 years of the nineteenth century. The other three southern localities (Table 9) are considerably more suspicious. Each is isolated from all other sites and each is in one of the southernmost counties. The Franklin County locality would have provided suitable habitat, but neither the Lancaster County nor Philadelphia County sites would have appropriate habitat.

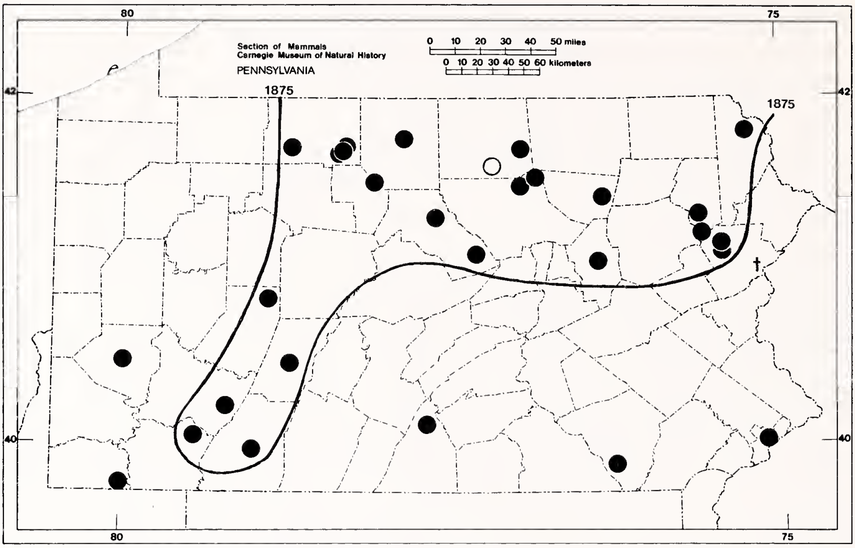

Fig. 9.—Map of Pennsylvania showing location of records of *Lynx canadensis.* Symbols used are described in Fig. 1.

There may be several reasons for the southwestern distribution of the species. One explanation is that between 1860 and 1900, nearly 7 million acres of mature forests were logged in Pennsylvania (Illick, 1923). Possibly some individuals were pushed or isolated in the Allegheny Mountains as prime habitat was destroyed. Another explanation is that the occurrence of *L. canadensis* is related to the distribution and population density of the snowshoe hare, a primary food source (Dalby, 1985; Godin, 1977). The population of the lynx may have experienced periodic upsurges during periods of high *Lepus* density in Pennsylvania. It is also possible that the similarities between bobcat and lynx caused some lynx to be misidentified, particularly if their occurrence was sporadic. However, the opposite supposition, that large bobcats were being incorrectly labeled lynx, has more frequently been the assumption.

The single museum specimen, the identification of which has been verified, was collected 10 November 1923 in Tioga County. This is the most recent record of the species in the Commonwealth and it postdates the last historical record by 20 years. It lends credence to the identifications in historical records from the northern counties.

The skeletal remains of *Lynx canadensis* in Monroe County and the known specimen collected at Antrium in Tioga County (Table 9; Fig.

9) verify the presence of this species in Pennsylvania. Whether the historical records represent an established species in typical habitat or the invasion of a cyclic population is a matter of conjecture. This question is particularly difficult to answer due to the availability of only a single verified specimen since the time of Rhoads (1903).

***Lynx rufus*—bobcat**

Lynx rufus has been referred to by a number of common names including the bay lynx, wild cat, bobcat, catamount, mountain cat, and tiger cat (Rhoads, 1903; Seton, 1929*a*; Warren, 1897*b*). Because *Lynx canadensis* has also been called gray wild cat, lynx, and catamount, a great deal of confusion has arisen surrounding accounts of these two species. In addition, the name catamount has also been applied to the mountain lion. To further confuse the situation, the term most often used for *Lynx rufus* during the nineteenth century was "wild cat." Yet this term is so generic that it may refer to a feral house cat as well as any other wild felid in Pennsylvania. Thus, differentiation between references to "wild cats" and "wildcats" was necessary. The similarity of the appearances of *Lynx rufus* and *L. canadensis* compounds the problem. Descriptions aimed at proving the capture of one or the other animal often concentrated on external characters, which are not diagnostic (see account for *Lynx canadensis*).

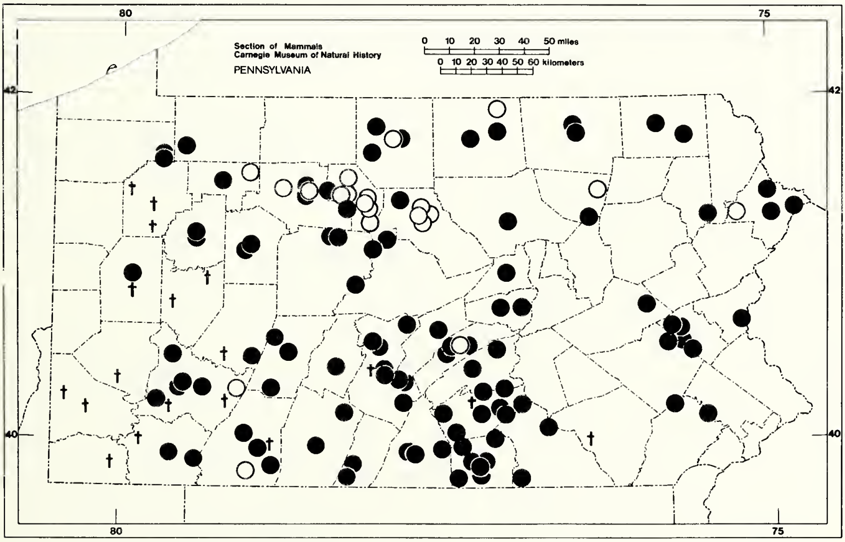

Fig. 10.—Map of Pennsylvania showing location of records of *Lynx rufus*. Symbols used are described in Fig. 1.

Table 10.—*Paleo-archaeological, historical, and specimen records of* Lynx rufus *from Pennsylvania.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
Recent	Cumberland Co., Carlisle caves	Skeletal parts found by S. F. Baird	Miller, 1940
N.D.	Armstrong Co., East Franklin Twp., Walkchalk Rockshelter (36Ar15)	Skeletal parts	Guilday et al., 1980
N.D.	Armstrong Co., Mahoning Twp., Wadding Rockshelter (36Ar21)	Skeletal parts	George and Bassinger, 1975; Guilday et al., 1980
N.D.	Fayette Co., Redstone Twp., Campbell Site (36Fa26)	Skeletal parts	Guilday et al., 1980
N.D.	Venango Co., Canal Twp., Venango Manor (36Ve18)	Skeletal parts	Guilday et al., 1980
N.D.	Venango Co., Scrubgrass Twp., Counterfeiters Cave (36Ve30)	Skeletal parts	Guilday et al., 1980
N.D.	Washington Co. North Strabane Twp., Boyle Site (36Wh19)	1 skeletal part, representing 1 individual	Nale, 1963
N.D.	Westmoreland Co., Sewickley Twp., Janitor Site (36Wm21)	Skeletal parts	Guilday et al., 1980
11,300 ± 700 BP	Washington Co., Jefferson Twp., Meadowcroft Rockshelter (36Wh297)	7 skeletal parts (*Lynx* cf. *rufus*)	Guilday et al., 1980
Pre-4000 BC	Huntingdon Co., W bank Raystown Branch, Juniata R., Sheep Rock Shelter (36Hu1)	6 skeletal parts representing 1 individuals (*Lynx* cf. *rufus*)	Guilday and Parmalee, 1965
100 BC–900 AD	Venango Co. Sandy Cr. Twp., 3 mi SE Franklin, Quaker State Rockshelter (36Ve27)	Skeletal parts	Guilday and Tanner, 1962
1190 AD	Somerset Co., Summit Twp., Gnagey Site (36So55)	Skeletal parts	George, 1983
1200–1400 AD	Greene Co., 4½ mi S Waynesburg, Varner Site (36Gr1)	5 skeletal parts (*Lynx* cf. *rufus*)	Guilday, 1961*b*

Table 10.—*Continued.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
1300–1500 AD	Allegheny Co., Stowe Twp., McKees Rocks Village Site (36A116)	5 skeletal parts representing 2 individuals (*Lynx* cf. *rufus*)	Guilday, 1961*a*; Lang, 1968
1390 ± 105 AD	Butler Co., Summit Twp., Bonnie Brook Site (36Bt43)	1 skeletal part representing 1 individual	Guilday et al., 1980; Herbstritt, 1981
1500–1600 AD	Indiana Co., Blairsville, Johnston Site (36In2)	5 skeletal parts	Guilday, 1955
1600–1625 AD	Lancaster Co., Washington Boro, 3 mi S Columbia, Eschelman Site (36La12)	35 skeletal parts representing 5 individuals	Guilday et al., 1962
1758–1766 AD	Westmoreland Co., Fort Ligonier (36Wm71)	3 skeletal parts representing 1 individual (*Lynx* cf. *rufus*)	Guilday, 1970
	HISTORICAL RECORDS		
1784	Montgomery or Chester Co., near Schuylkill R.	1 killed by R. Miller	Pennypacker, 1872
1805	Bradford Co., Wyoming Valley	28 killed by 600 hunters	Heverly, 1926
1817	Northampton Co., Easton	1 killed	Watson, 1844
1820	Chester Co., French Cr.	1 killed by W. and J. Vanderslice	Pennypacker, 1872
1830	Dauphin Co., vicinity Lykens Valley	2 killed	Hazard, 1830*b*
1831	Huntingdon Co.	13 killed	Hazard, 1832
1832	Bradford Co., 4 mi N Towanda	1 killed by C. Brown during March	U.S. Gazette, 30 Nov 1831; Hazard, 1832
1835	York Co., Conowago Hills, ½ mi from York Haven	1 killed on 17 Jan	York Gazette, 17 Jan 1835; Hazard 1835
1835–1842	Butler Co.	Bounties paid on 67 mountain lions	Webb and Stevens, 1934
1843	Berks Co., Greenwich Twp.	1 killed by D. Hehn	Pennsylvania Telegraph, 6 Dec 1843
1849	Dauphin Co., Manada Furnace	3 killed between Feb. and Dec	Pennsylvania Telegraph, 19 Dec 1849
1853	Perry Co., Millerstown, foothills of Tuscarora Mts.	1 killed by train	Tuscarora Register, 27 Jan 1853
1853	Schuylkill Co., near Tamaqua	1 killed by J. Haughawout in Sept	Lebanon Advertiser, 21 Sept 1853

Table 10.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1856	Westmoreland Co., Hempfield Twp., near county poorhouse	1 killed by S. Reamer	Greensburg Democrat, 16 Dec 1856
1857	Westmoreland Co., 3 mi from Greensburg, Sewickley Cr.	1 killed by J. Wentzel	Greensburg Democrat, 6 Jan 1857; Harrisburg Telegraph, 6 Jan 1857
1858	Westmoreland Co., Unity Twp.	1 killed	Bedford Gazette, 12 Mar 1858
1858	Lycoming Co., Loyalsock Cr., near Williamsport	Several killed	Pennsylvania Telegraph, 26 Nov 1858
1959	Greene Co., Windham	1 killed by English terrier	Luzerne Telegraph, 5 Jan 1859
1859	Mifflin Co., Derry Twp., Shade Mt.	1 killed on 3 Jan	True Democrat, 13 Jan 1859
1859	Columbia Co., North Mt.	1 killed by party of hunters in July	American Volunteer, 14 Jul 1859
1860	Juniata Co., a few miles below Mifflin	1 killed by train	Pennsylvania Daily Telegraph, 12 Jan 1860
1860	Cumberland or Perry Co., above Sterrett's Gap	1 killed by E. Mather in Feb	Carlisle Herald, 22 Feb 1860
1860	Cumberland Co.	1 killed by soldier in May	American Volunteer, 17 May 1860
1860	Cumberland Co., 1 mi S Mechanicsburg	1 killed by D. Durnbaugh on 10 Oct	Pennsylvania Daily Telegraph, 13 Oct 1860; American Volunteer, 18 Oct 1860; repr. from Mechanicsburg J.
1860	Cumberland Co., Southampton Twp.	1 killed by R. Bomberger in Nov	Daily Telegraph, 12 Nov 1860
1860	Cumberland Co. (northern part)	1 killed by party of hunters in Dec	Patriot and Union, 21 Dec 1860
1861	Cumberland Co., near Lisburn	1 killed by Preston and Haehnlen in Nov	Patriot and Union, 30 Nov 1861
1862	Lehigh Co., Weisenburg Twp. or Upper Macungle Twp.	1 killed by A. Brauss	Pennsylvania Daily Telegraph, 20 Nov 1862; Central Press, 28 Nov 1862
1865	Jefferson Co., Penn Mills	1 killed by S. Boring in Aug	Patriot Daily Union, 16 Aug 1865

Table 10.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1865	Adams Co., near Gettysburg	1 killed by F. Will in Nov	Daily Telegraph, 7 Dec 1865; repr. from Gettysburg Sentinel
1865	Adams Co., near Gettysburg at Weigle's Dam	1 killed by K. Cullison in Dec	Daily Telegraph, 7 Dec 1865; repr. from Gettysburg Sentinel
1865	Snyder Co., Freeburg	1 captured by S. Roush	Patriot and Daily Union, 19 Dec 1865
1867	Huntingdon Co., Warrier Ridge, near Smithfield	1 killed by E. Westbrook in Jan	Journal and American, 16 Jan 1867
1867	Adams Co., Straban Twp.	1 killed by W. Cashman in Feb	Harrisburg Daily Telegraph, 12 Feb 1867
1867	Dauphin Co., Stony Cr., near Ellendale Forge	2 killed by W. P. Kinger in March	Harrisburg Daily Telegraph, 26 March 1867
1867	Huntingdon Co., above Mount Union, at Narrows, (Jack's Mt.)	1 killed by T. Farmer in Nov	True Democrat, 27 Nov 1867
1867	Bedford Co., Hopewell Twp., between Harbor Mt. and Broad Mt.	1 killed by J. M. McClure in Dec	Bedford Gazette, 13 Dec 1867
1868	Westmoreland Co., Washington Twp.	1 killed by H. Hartman	Greensburg Herald, 5 Feb 1868
1869	Susquehanna Co., Lenox	1 killed in Dec	Blackman, 1873
1869	Lehigh Co., Steinville	1 killed by E. Shaffer	Patriot, 4 Mar 1869
1870	Somerset Co., Berlin	1 killed in Dec	Bedford Gazette, 8 Dec 1870
1872	Adams Co., Huntingdon Twp.	1 killed in July	Harrisburg Daily State J., 22 Jul 1872
1873	Centre Co., near Philipsburg Loch Lomond sawmill	3 killed	Clearfield Raftsman's J., 10 Dec 1873
1874	Juniata Co.	1 captured by J. Tyson in Jan	Huntingdon Globe, 13 Jan 1874
1874	Cambria Co.	1 killed in May	Huntingdon Globe, 19 May 1874
1875	Clearfield Co., Lawrence Twp.	1 killed by W. P. Fulton in Feb	Clearfield Raftsman's J., 24 Feb 1875

Table 10.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1875	Huntingdon Co.	1 killed by A. Park in Feb	Huntingdon Globe, 2 Mar 1875
1875	Huntindon Co., Jackson Twp.	1 killed by S. Wilson	Huntingdon Monitor, 9 Mar 1875
1875–1876	Blair Co., Frankstown Twp.	14 killed between Dec and Apr	Huntingdon Monitor, 5 Apr 1876
1876	Clearfield Co., Goshen Twp., Lick Run	1 killed by G. Selfridge	Clearfield Raftsman's J., 2 Feb 1876
1876	Perry Co.	1 killed in Dec	Harrisburg Daily Patriot, 15 Dec 1876
1876	Potter Co.	8 killed	Harrisburg Daily Patriot, 25 Apr 1876
1877	Franklin Co.	1 killed by S. Burgher	Shippensburg News, 6 Jan 1877
1878	Cumberland Co., South Middletown Twp.	1 killed by F. Thomas in Jan	Huntingdon J., 1 Feb 1878
1878	Huntingdon Co., near Mount Union	1 killed by Miller in Sept	Huntingdon J., 13 Sep 1878
1878	York Co., West Manheim Twp.	1 killed by P. J. Barnhart in Oct	York Daily, 11 Oct 1878
1878	Snyder Co., Franklin Twp.	1 killed by J. Coleman in Nov	Snyder County Tribune, 7 Nov 1878
1878	Franklin Co., St. Thomas Twp.	1 killed in Dec	Shippensburg News, 28 Dec 1878
1878	Adams Co., Fountain Dale	1 killed	Huntingdon J., 5 Apr 1878
1878	Huntingdon Co.	Bounties paid	Huntingdon Monitor, 30 Jan 1879; Daily New Era, 15 Feb 1879
1878	Huntingdon Co., Cromwell Twp.	2 killed by J. A. Rogers	Huntingdon Monitor, 14 Mar 1878; Huntingdon J., 15 Mar 1878
1879	Lehigh Co., Blue Mt., Steinville	1 killed by J. Lichty in July	Allentown Democrat, 30 Jul 1879
1879	Clarion Co.	Bounties paid	Harrisburg Telegraph, 3 Mar 1880; Weekly Telegraph, 10 Mar 1880
1879	Juniata Co.	1 killed	Huntingdon Monitor, 11 Dec 1879

Table 10.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1880	Adams Co., Narrows Hill	1 killed by S. Hewitt on 5 Jan	Shppensburg News, 21 Feb 1880
1880	Adams Co., Bear Mt.	1 killed by J. Hewitt on 12 Jan	Shippensburg News, 21 Feb 1880
1880	Cambria Co., Paint Twp., Scalp Level	2 killed by J. Baumgardner and K. Kunkle in Dec	Huntingdon J., 10 Dec 1880
1880	Tioga Co., (Block House)	1 killed	Industrial Register, 19 Feb 1880
1881	Tioga Co., Lambs Cr.	1 killed	Blossburg Industrial Register, 20 Jan 1881
1881	Westmoreland Co., Sewickley Twp.	1 killed	Tribune Herald, 7 June 1881
1882	Cumberland Co., 2 mi W Newburg	1 killed by M. Brechbiel in Dec	Shippensburg News, 30 Dec 1882
1882	Franklin Co., S of Greenwood	1 killed by C. Reinhart	Shippensburg News, 29 Apr 1882
1882	Franklin Co., 1 mi E Fayetteville	1 killed by W. Crawford	Shippensburg News, 29 Apr 1882
1889–1896	Huntingdon Co.	18 killed by G. F. Smith	Bellefont Democrat, 3 Dec 1896; Warren, 1897*b*
1890	Jefferson Co., near Reynoldsville	1 killed	Elliott, 1894
1892	Elk Co., St. Mary's	1 killed by Senator H. A. Hall	Warren, 1897*b*
1895–1896	Huntingdon Co., Alexandria	1 killed by J. P. Swope	Huntingdon Globe, Jan 1896; Warren, 1897*b*
1896	Jefferson Co., Reynoldsville	15 killed by E. C. Lewis	Warren, 1897*a*, 1897*b*
1903	Allegheny, Armstrong, Beaver, Bucks, Butler, Chester, Crawford, Delaware, Erie, Mercer, Montgomery, Philadelphia and Washington cos.	Bobcat thought to be extirpated	Rhoads, 1903
1906	Crawford Co., S of Titusville	1 killed	Titusville Herald, 5 March 1908
1908	Crawford Co., Titusville	1 killed by T. Burns, F. Lang, and S. Chambers	Titusville Herald, 5 March 1908
1924	Berks-Lehigh Co. border	1 killed	Roberts and Early, 1952

Table 10.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1927	Bedford Co., Martin Hill	15 killed by O. Smith	Roberts and Early, 1952
1937	Fulton Co., 9 mi N Maryland border, Town Hall Mts.	Record size bobcat killed by O. Smith	Roberts and Early, 1952
1939	Clinton Co., Renovo	1 captured by G. Cross, used in film made by Game Commission	Anon., 1939*a*
1940	Columbia Co., Jamison City near Refuge No. 13	1 killed	Anon., 1941
1941	Cameron Co., vicinity Vandergrift	1 killed by R. Porreca on 4 Dec	Anon., 1943
1943	Fulton Co., State Game Land #65	1 killed by O. Smith	Robert and Early, 1952
1945	Pike Co., vicinity Milford	1 trapped by J. Flader in Oct	Lohman, 1945
1946	Cambria Co., Black Lick Twp.	1 killed in Nov; reported by N. M. Rhua	Grimm and Roberts, 1950
1946	Warren Co., Selkirk	1 hit by car; found by Game Protector in Nov	Miller, 1947
1948	Fayette Co., Dunbar Twp.	1 killed in Jan; reported by T. W. Meehan	Grimm and Roberts, 1950
1948–1949	Indiana Co., Buffington Twp.	1 killed in Dec or Jan; reported by G. A. Miller	Grimm and Roberts, 1950
1949	Fayette Co., 5 mi NW Confluence	1 killed in Jan; reported by L. B. Welch	Grimm and Roberts, 1950
1952	Elk Co., vicinity St. Mary's	2 shot; 2 seen by E. Vollmer and J. Gradl	Anon., 1952
1955	Potter Co., Keating Twp.	1 shot by Game Protector on 8 Dec	Stidd, 1956
1956	Susquehanna Co.	Roadkill picked up and tanned by F. Maby in July	Day, 1956
1957	Elk Co., Dents Run	1 caught in March and kept alive by R. Harrison	Servey, 1957
1957	Cameron Co., Steam Mill Pine	1 female observed, 4 kittens collected by R. Mason in May	Erickson, 1957
1957	Somerset Co., near Glencoe	1 killed by D. Michaels on 12 Sept	Cox, 1957

Table 10.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1957	Somerset Co., vicinity Somerset	2 killed	Cox, 1957
1959	Clinton Co., vicinity Kettle Cr.	1 trapped by C. Cross in March	Keiper, 1959
1962	Potter Co., vicinity Coudersport	1 trapped by I. Haskins	Anon., 1962
1964	Lackawanna Co., Freystown	1 killed by L. Grim	Anon., 1964
1968	Centre Co., Sterling Run	1 killed by Walters	Sloan, 1968
1968	Centre Co., Moores Run	1 killed	Sloan, 1968
		SPECIMEN RECORDS	
About 1900	Clinton Co., Renovo	RPMAG 1754 skin; RPGAM 1755–56 skin and skull	RPMAG 1754–1756; Reading Public Museum and Art Gallery
1903	Forest Co., head of Blue Jay Cr.	Skin collected by J. Godell on 12 Jan	CM 1256; Carnegie Museum Natural History
1905	Sullivan Co., Lopez	Specimen killed by 1 Feb	ANSP 12067; Philadelphia Academy of Sciences
1906	Cameron Co.	Killed 12 Oct; skull preserved	USNM 249898; U.S. National Museum of Natural History
1913	Juniata Co., Mifflin	Collected by G. L. McCartney in Feb; skin preserved	CM 2593; Carnegie Museum of Natural History
1915	Cameron Co.	Collected by G. A. Link on 24 Nov and 8 Dec; preserved as skin and skull	CM 3224 and 3226; Carnegie Museum of Natural History
1915	Cameron Co., Hicks Run	Collected by J. M. Phillips party on 24 Dec; preserved as skeletons	CM 3230–3232; Carnegie Museum of Natural History
1918	Cameron Co., Sinnamahoning	Collected on 24 Jan; skull preserved	WPMM M407; William Penn Memorial Museum
1934	Clinton Co., 15 mi N Renovo, State Game Refuge #7	Collected by B. J. Davis on 30 March; preserved as skin,	CM 8585; Carnegie Museum of Natural History

Table 10.—*Continued.*

Date	Locality	Comments	References
		SPECIMEN RECORDS	
		skull and body skeleton	
1934	Somerset Co., 10 mi SW Meyersdale	Collected by M. Folk on 5 Aug; preserved as skin, skull and body skeleton	CM 10151; Carnegie Museum of Natural History
1940–1945	Westmoreland Co., vicinity Ligonier and Laughlintown	Collected by G. A. Link; preserved as skull	CM 57505; Carnegie Museum of Natural History
1941	Potter Co.	Collected by H. J. Clement on 9 Nov; skull preserved	CM 20704; Carnegie Museum of Natural History
1949	Pike Co., 5 mi SE Greentown	Collected by Grimm and Rutledge, Pennsylvania Mammal Survey on 28 Aug; skin and skull preserved	CM 36297; Carnegie Museum of Natural History
1949	Cameron Co., near Emporium	Collected by Erickson during the autumn; skull preserved	CM 61331; Carnegie Museum of Natural History
1953	Elk Co., St. Mary's	1 killed by J. Kosinski on 10 Dec; skeleton preserved	CM 61363; Carnegie Museum of Natural History
1956	Elk Co., Ridgeway Twp.	Collected on 20 Oct; preserved as body mount	PSU M889; Pennsylvania State University
1962	Tioga Co., 3 mi N Tioga	Collected 10 June; skull preserved	GMU 224; George Mason University
1971	Lancaster Co., Peach Bottom	Body mount	Franklin and Marshall College (unnumbered)

Faunal remains of a *Lynx* comparable in size to *L. rufus* are very common, particularly in southwestern Pennsylvania (Guilday, 1955, 1961*a*, 1961*b*; Guilday and Parmalee, 1965; Guilday et al., 1962, 1980; Herbstritt, 1981; Lang, 1968; Miller, 1940; Nale, 1963). The bobcat was also common throughout Pennsylvania a century ago (Doutt et al., 1973). Bounties were paid by county or Commonwealth decree almost continuously between 1810 and 1938. An examination of annual bounty payments during this century shows a high of 792 specimens in 1915–1916 (Anon., 1939*b*). For the next ten years, the bounty counts appear to show cyclic periodicity. However, between 1927–1928 and 1937–1938, the decline in numbers was steady, resulting in the repeal of the bounty on bobcats in October of 1938 (Anon., 1939*b*). Doutt et al. (1973) believed that fewer than 100 bobcats existed in the Commonwealth by the mid-1960's and that the distribution was limited to isolated mountainous areas. In adjoining states, a decline in numbers has also been noted with any occurrence being restricted to isolated regions (Bailey, 1946; Dekay, 1842; Gottschang, 1981; McKeever, 1954; Paradiso, 1969).

Historical records dating as far back as 1784, and museum specimens collected in Pennsylvania since 1900, have been mapped (Fig. 10). Recent collecting localities largely reflect this clustering of the species in forested and mountainous areas. The Pennsylvania Mammal Survey, conducted between 1947 and 1951, divided the Commonwealth into six regions. Reports from these individual regions (Table 10) suggest that the distribution of the bobcat had become limited to the more isolated portions of each district (Gifford and Whitebread, 1952; Grimm and Roberts, 1950; Grimm and Whitebread, 1952; Richmond and Roslund, 1949; Roberts and Early, 1952; Roslund, 1951). The bobcat was not discussed in the report for the northwestern region (Richmond and Roslund, 1949), but it was included on a checklist for that region. Thus, the status of the species is in question, although its presence in the Commonwealth is not.

It is interesting to note (Fig. 8A and Fig. 10) the complementarity of the mountain lion and bobcat locality records. Further comparison of these data indicates that many more bobcats were reported during the last half of the nineteenth century than during the first half, even though the mountain lion was actively reported during the earlier period. It must be realized that both of these observations may be an artifact of man's settlement of the Commonwealth during the 1800's.

Alces alces—moose

When French Canadian fishermen first encountered the moose, they correctly identified it as a member of the deer family (Merrill, 1916), and applied the Basque name for deer—orenac—to this animal. This was eventually corrupted to "orignac" and "orignal." In Pennsylvania the name was further altered to "original." This title eventually led to the supposition that the moose was the basic stock from which all other members of the deer family arose (Shoemaker, 1919).

O'Connor and Goodwin (1961) point out that *Alces alces* is actually an elk and is known by that name in the Old World. Early British settlers probably knew that the European elk was a large deer, but few had ever actually seen one. Thus, upon seeing the native American wapiti (*Cervus elaphus*), they named the animal "elk." Later, when the North American relative (*Alces alces*) of the European elk was observed, the name "elk" was already in use. The current day common name which we give to *Alces alces* is derived from any of a number of Algonquin Indian dialects. Spellings range from moos, mos, mus, monz, moosh, and mons, to monswa, and each means "he strips or eats off" to describe the eating of bark and twigs (Merrill, 1916). In early Pennsylvania literature, the moose is most often referred to as "black moose" to distinguish it from the "gray moose," a name often used for the elk (*Cervus elaphus*) (Shoemaker, 1919). Thus, even if old place names could be accepted as evidence of this animal's presence in the area, it might be difficult to tell to which animal the reference applied.

The presence of moose in Pennsylvania has been described in general terms by numerous authors who include the Commonwealth as the southernmost part of its range in eastern North America (Goodwin, 1936; Hall, 1981; O'Connor and Goodwin, 1961; Shoemaker, 1912, 1919; Schoepf, 1793). The range maps of Hall (1981) are based on Goodwin's (1936) quotation of J. D. Schoepf's (1793) "Travels in the Confederation." Schoepf, a naturalist who travelled in North America in 1783 and 1784, apparently drew information from the local populace. Shoemaker (1912, 1919) has contributed a considerable amount of information to the supposition that moose roamed the Commonwealth during historic times. It should be noted that Shoemaker (1919) specifically labelled some of his accounts as folklore and credits Rhoads (1903) with covering the subject in a scientific manner. Hunters' stories recounted by Shoemaker (1919) include one by John Q. Dyce who describes a migration path across the west branch of the Susquehanna River near Renovo, Clinton County, to the present town of Clearfield, then along the Allegheny summits to Somerset and from there into Maryland. Another hunter, Josiah Roush, described a similar path, but marked the origin of the moose in Pennsylvania near Narrowsburg on the Delaware River (Shoemaker, 1919). Wind Gap in Northampton County, 10 miles from Marten's Creek on the Delaware River, has been described as the site of the demise of individual moose on several occasions (Collins, 1933; Shoemaker, 1919; Walker, 1959).

However, Shoemaker (1947) states that " no trustworthy information has come to light to indicate that the moose did breed in Pennsylvania." He also believed it to be a "well established fact that the Black Moose has not been a permanent resident in Pennsylvania during the past five hundred years," nor is it even "an annual visitor." Rhoads (1903) omitted moose from his list of mammals of Pennsylvania. He discussed a theory that the moose may have wandered into the Commonwealth during late pre-Columbian times, but seems to consider it improbable, or at least feels that the theory lacks proof.

Peterson (1955) provides insight regarding post-Pleistocene movement. During the greatest extent of Wisconsin glaciation, moose distribution apparently extended as far south as South Carolina. Post-glacial (7500–9000 BP) dispersion of the moose into these northern regions was slow. Peterson (1955) indicates that there have been major movements northward since 1875 and describes the southern reaches of its range by that time to be central New York. In attempting to explain the lapse in movement between the disappearance of the ice and 1875, he cites several possible reasons. Part of the time may have been needed for the establishment of appropriate habitat through forest succession. A slight, general Holarctic warming trend occurred during the last century and population pressure may have affected the pattern of repopulation (Peterson, 1955). Habitat disturbances caused by logging and fire may explain the sudden dispersal.

Peterson's timetable seems to fit well with the reported records of moose sightings and kills in Pennsylvania. Dates listed for "last moose" in the Commonwealth center around 1790–1805 and would have allowed ample time for the retreat to central New York state by 1875. Habitat in the northern tier counties of Pennsylvania would have been suitable until well after the end of the eighteenth century (Illick, 1923). O'Connor and Goodwin (1961) indicate that although the moose is well equipped for long distance movement, an individual may be content to spend its entire life within a five-square-mile area. This information would tend to negate stories of regularly travelled migration paths throughout the Commonwealth. It may also help to explain why major movement did not occur until population, habitat, and possibly even climatic conditions forced redispersal.

There are no references to moose being among the fauna of Ohio (Brayton, 1882; Gottschang, 1981), Maryland (Paradiso, 1969), West Virginia (McKeever, 1954), or New Jersey (Rhoads, 1903). DeKay (1842) indicates that moose could still be found in the unsettled New York counties of Essex, Franklin, Hamilton, Herkimer, Lewis, and Warren in the northern part of that state. By 1874, the moose was considered rare in the Adirondacks, and a report to the New York Legislature requested a complete ban on moose hunting (Shoemaker, 1919).

Another factor that may have a serious impact on the distribution of the moose is the brain worm, *Parelaphostrongylus tenuis* (Karns, 1967). Karns (1967) states that this nematode occasionally parasitizes the moose and is not well tolerated. Kearney and Gilbert (1976) state that this meningeal worm is "enzootic in the white-tailed deer population in much of the eastern North America and has been recognized as an important agent in the decline of moose populations in this area" (see account for white-tailed deer). Historical evidence of this "cerebrospinal nematodiasis" can be traced to moose deaths in the 1920's and 1930's in Minnesota where deer populations were very high. Karns (1967) believes *P. tenuis* could represent a major factor in the decline

Table 11.—*Paleontological and historical records of* Alces alces *from Pennsylvania.*

Date	Locality	Comments	References
	PALEONTOLOGICAL RECORD		
Pleistocene	Bucks Co., <1 mi S Rieglesville, Durham Cave	Skeletal remains found about 1847	Shoemaker, 1919
	HISTORICAL RECORDS		
N.D.	Northampton Co., Windgap	J. Heller watched moose die after being chased by dogs; may be same as 1803 record	Walker, 1959
Pre-1776	Somerset Co., Elk Lick	Moose seen	Walker, 1959
1780–90	Mifflin Co., near McVeytown McVeytown, south of Juniata R.	1 killed by Buchannan	Walker, 1959
Pre-1790's	Centre Co.	Indians killed moose	Shoemaker, 1919
About 1800	Clinton Co. (northern part)	J. Smoke and S. Nelson report moose visited area until about 1800	Shoemaker, 1929
1803	Northampton Co., Windgap	"Last moose" killed	Collins, 1933
1805	Clinton Co., Fish Dam Run	T. Poorman killed "last moose" while in the company of State Surveyors and P. Pentz, a Ranger	Shoemaker, 1929
1819	McKean Co., Bradford at Washington Park	J. Jacobs found a "fresh" set of antlers	Walker, 1959
1850	Clinton Co., Tamarack Swamp	J. Hennessy found antlers of either moose or caribou	Shoemaker, 1919

of the moose population in Minnesota; thus, the relationship between *Alces, Odocoileus,* and *Parelaphostrongylus* may have affected moose distribution in Pennsylvania.

There are no museum specimens of the moose from Pennsylvania in Recent mammal collections. However, Pleistocene remains of moose were found about 1847 at Durham Cave near Riegelsville (Table 11; Fig. 11) in Bucks County (Leidy, 1889). Recent moose antlers were reported to have been found in McKean County in 1819 and Clinton County in 1850, but neither of these finds produces a timetable for the presence of the moose during historic times.

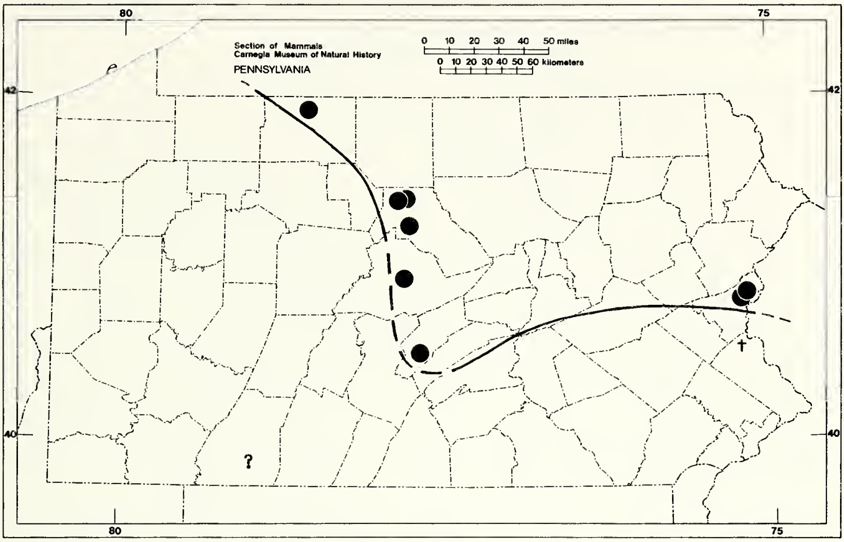
Section of Mammals
Carnegie Museum of Natural History
PENNSYLVANIA
0 10 20 30 40 50 miles
0 10 20 30 40 50 60 kilometers
80
75
42
40
?

Fig. 11.—Map of Pennsylvania showing location of records of *Alces alces*. Symbols used are described in Fig. 1.

In essence, the Durham Cave material establishes the presence of moose in Pennsylvania during the Pleistocene. Peterson's (1955) description of post-glaciation redispersal explains the retreat of the moose from Pennsylvania. The fact that only four reports of moose kills have persisted seems to establish the scarcity of the animal in Pennsylvania during historic times. Such reports by hunters show that only the earliest settlers to the Commonwealth may have had an opportunity to see the moose. However, the proliferation of place names involving moose has led to the mistaken impression that this animal was a common member of the fauna of Pennsylvania during colonial times.

***Cervus elaphus*—wapiti**

Cervus elaphus is correctly called the wapiti. It is also known as elk, American elk, American red-deer, and in colonial times was referred to as "grey moose" (Seton 1929*c*; Shoemaker, 1919; see account for moose). Its comparatively larger size and characteristic rump-patch should make it easy to distinguish from other Pennsylvania mammals. However, historical accounts suggest it was not as well known as many of the other species.

The distribution of *C. elaphus* in the eastern United States ranged from northern New York to central Georgia (Hall, 1981; Murie, 1951).

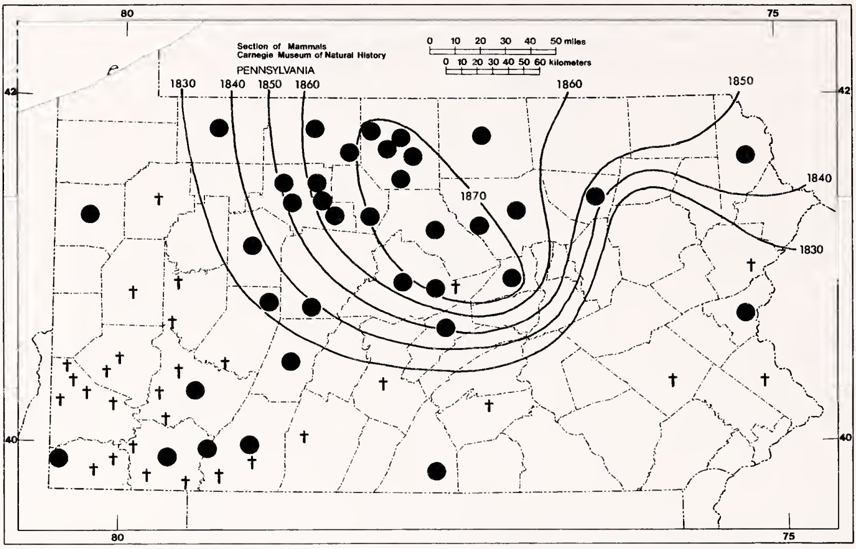

Fig. 12.—Map of Pennsylvania showing location of records of *Cervus elaphus*. Symbols used are described in Fig. 1.

Throughout this area the wapiti occurred in a variety of habitats, but Banfield (1974) reports a preference for "open areas such as alpine pastures, marshy meadows, river flats, open prairies, and aspen parkland."

Before man's influence, the wapiti probably occurred in all parts of Pennsylvania with higher concentrations existing in the Allegheny Mountains. This distribution is supported by paleo-archaeological and historical records (Fig. 12; Table 12). By the end of the eighteenth century, the distribution in Pennsylvania had already been significantly reduced (Gerstell, 1936*a*; Murie, 1951). After 1830, records of *C. elaphus* were restricted to localities northeast of Jefferson and Clearfield counties. Populations existed in the northeast corner of the Commonwealth in the Poconos of Wayne County until 1830 to 1845 (Gerstell, 1936*a*; Murie, 1951; Rhoads, 1903). About this time J. Audubon used two individuals of wapiti from western Pennsylvania in his book *The Viviparous Quadrupeds of North America* (Rhoads, 1903). By 1860, the wapiti was probably restricted to the northcentral part of Pennsylvania. The last records are from the 1870's and include Potter, Clinton, Centre, and Union counties. By this time the wapiti probably consisted of only a very few individuals. Some authors (Gerstell, 1936*a*; Rhoads, 1903; Seton, 1929*c*; Warren, 1897*a*) give credit to a Seneca

Table 12.—*Paleo-archaeological, historical, and specimen records of* Cervus elaphus *from Pennsylvania.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
N.D.	Armstrong Co., East Franklin Twp., Walkchalk Rockshelter (36Ar15)	Skeletal remains	Guilday et al., 1980
N.D.	Armstrong Co., Mahoning Twp., Wadding Rockshelter (36Ar21)	Skeletal remains	Guilday et al., 1980
N.D.	Armstrong Co., South Buffalo Twp., Murphy's Old House Site (36Ar129)	Skeletal remains	Guilday et al., 1980
N.D.	Bucks Co., less than 1 mi S Riegelsville, Durham Cave	Skeletal fragments	Hay, 1923; Leidy, 1889; Rhoads, 1903
N.D.	Fayette Co., Springhill Twp., 3 mi S Monongahela R and 1½ mi S George's Cr., Phillips Site (36Fa22)	Skeletal remains	Gilmore, 1946; Guilday et al., 1980
N.D.	Fayette Co., 4 mi S Somerfield, Henry Clay Twp., Martin Site, (36Fa23)	Skeletal remains	Gilmore, 1946; Guilday et al., 1980
N.D.	Greene Co., Cumberland Twp., Hartley Site (36Gr23)	Skeletal remains	Guilday et al., 1980
N.D.	Somerset Co., 4 mi E Confluence, Addison Twp., Fort Hill Site (36So2)	Skeletal parts	Gilmore, 1946; Guilday et al., 1980
N.D.	Venango Co., Venango Manor #1, (36Ve18)	Skeletal remains	Guilday et al., 1980
N.D.	Venango Co., Scrubgrass Twp., Counterfeiters Cave (36Ve30)	Skeletal remains	Guilday et al., 1980
N.D.	Washington Co., North Strabane Twp., Boyle Site (36Wh19)	Skeletal remains	Guilday et al., 1980; Nale, 1963
N.D.	Washington Co., Hanover Twp., Scarem Site (36Wh22)	Skeletal remains	Guilday et al., 1980; Mayer-Oakes, 1954

Table 12.—*Continued.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
N.D.	Washington Co., Jefferson Twp., Moore Farm Site (36Wh38)	Skeletal remains	Guilday et al., 1980
N.D.	Washington Co., Union Twp., Mathies Mine Village Site (36Wh54)	Skeletal remains	Guilday et al., 1980
N.D.	Westmoreland Co. Sewickley Twp., Janitor Site (36Wm21)	Skeletal remains	Guilday et al., 1980
N.D.	Westmoreland Co. South Huntingdon Twp., Smithton Site (36Wm70)	Skeletal remains	Guilday et al., 1980
N.D.	York Co.	Several foot bones and head of femur	Rhoads, 1903
Quaternary	Monroe Co., 2½ mi SW Stroudsburg, Hartmans Cave (=Crystal Hill Cave)	Skeletal fragments	Leidy, 1889; Rhoads, 1903
Recent	Cumberland Co., near Carlisle, Carlisle caves	Skeletal fragments	Miller, 1940
Recent	Bedford Co., West St. Clair Twp., 1.5 mi SE New Paris	Skeletal fragments	Guilday and Bender, 1958
Recent	Berks Co., Popular Neck Rock Shelter	Skeletal remains	Poole, 1939
11,300 ± 700 BP	Washington Co., Jefferson Twp., Meadowcroft Rockshelter (36Wh297)	37 skeletal parts	Guilday et al., 1980
9300–7290 BC	Centre Co., Hosterman's Pit	1 skeletal part representing 1 specimen	Guilday, 1967
pre-4000 BC	Huntingdon Co., W bank Raystown Branch of Juniata R., Sheep Rock Shelter (36Hu1)	33 skeletal parts representing 2 specimens	Guilday and Parmalee, 1965
100 BC–AD 900	Venango Co., Sandy Creek Twp., 3 mi SE Franklin, Quaker State Rockshelter (36Ve27)	28 skeletal parts	Guilday and Tanner, 1962

Table 12.—*Continued.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
1100 AD	Allegheny Co., Collier Twp., Drew Site (36Al62)	13 skeletal parts representing 1 specimen	Buker, 1970
1180 AD	Westmoreland Co., Penn Twp., Ryan Site (36Wm23)	7 skeletal parts	George, 1974
1190 AD	Somerset Co., Summit Twp., Gnagey Site (36So55)	156 skeletal parts	George, 1983
1200–1400 AD	Greene Co., 4½ mi W Waynesburg, Varner Site (36Gr1)	232 skeletal parts	Guilday, 1961*b*
1330 AD	Allegheny Co., Stowe Twp., McKees Rocks Village Site (36Al16)	71 skeletal parts	Lang, 1968
1390 ± 105 AD	Butler Co., Summit Twp., Bonnie Brook Site (36Bt43)	38 skeletal parts representing 1 specimen	Guilday et al., 1980; Herbstritt, 1981
1400–1525 AD	Fayette Co., Redstone Twp., Campbell Site (36Fa26)	Skeletal remains	Guilday et al., 1980
1500–1600 AD	Indiana Co., Blairsville, Johnston Site (36In2)	28 bone fragments	Guilday, 1955
1600–1625 AD	Lancaster Co., Washington Boro, 3 mi S Columbia, Eschelman Site (36La12)	1090 skeletal parts representing 21 specimens	Guilday et al., 1962
	HISTORICAL RECORDS		
N.D.	Franklin Co., Five Forks	Pair of antlers excavated in 1880 and estimated to be 150 years old	Shippensburg News, 6 Nov 1880
N.D.	Mercer Co.	2 antlers found in 1795–1797	Rhoads, 1903
N.D.	Clinton Co., Sugar Valley	"Coronet of an elk horn" excavated in 1817 and estimated to be about 100 years old	Shoemaker, 1929
1759	Northampton Co., Nazareth	1 killed	Shoemaker, 1919
1790	Fayette Co.	1 killed by Hechston	Grimm and Roberts, 1950
1794	Mercer Co.	1 killed	Rhoads, 1903
1795	Greene Co., Dunkard Cr.	1 killed	Grimm and Roberts, 1950

Table 12.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1816	Potter Co., near Kettle Cr.	1 captured by P. Tome, I. Lyman, G. Ayres, L. D. Spoffard, and W. Waters	Pittsburgh Post, 19 Apr 1896; Rhoads, 1903
1820	Centre Co.	1 killed by J. Earls; reported to be last killed in region	Linn, 1883
1820	Westmoreland Co.	1 killed by Lobengier	Grimm and Roberts, 1950
1824	Centre or Clinton cos.	5 killed by W. Hammersly	Linn, 1883; Lewistown True Democrat, 17 Dec 1874
1825	Somerset Co., Stoneycreek Glades	1 killed by F. Shank	Grimm and Roberts, 1950
About 1830	Sullivan Co., near Ringdale	1 killed by Wilcox and Northrup; reported to be last in region	Rhoads, 1903
1830's	Warren Co.	1 killed and mistakenly reported for Elk Co. in 1874	Seton, 1929*c*
1831–1837	Clinton, Potter, Tioga, and Lycoming cos.	Over 20 killed by S. I. Nelson	Murie, 1951; Rhoads, 1903; Shoemaker, 1929; Swank, 1908
1832	Jefferson Co.	5 killed by B. Long	Watson, 1844; Democratic Enquirer, 20 Dec 1832
1834	Jefferson Co.	1 captured by M. Long, W. Long, J. Long, and A. Vastbinder	McKnight, 1905*a*
1834	Lycoming and Tioga cos., headwaters Pine Cr.	13 killed	Rhoads, 1903
1835	Lycoming and Tioga cos., Pine Cr.	1 killed	Rhoads, 1903
1835	McKean Co., Norwich Twp., Colegrove Brook	2 killed by E. Dickinson	Rhoads, 1903
1837	Clearfield Co.; near Coalport	1 killed by J. Turner	Rhoads, 1903; Warren, 1897*a*
1839	Cameron Co., Driftwood about a mile from Big Elk Lick	1 killed by father of E. Dickinson	Rhoads, 1903

Table 12.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1839–1840	Wayne Co.	1 killed; reported by E. Teeple to be last killed in county	Rhoads, 1903
1845	Pocono Mts.	1 killed	Allen, 1942; Shoemaker, 1915*a*
1845–1846	Potter Co., headwaters of W Branch of Pine Cr.	1 killed; reported by E. O. Austin to be last killed in county	Rhoads, 1903
1847	Mifflin Co., Seven Mountains, Treaster Valley	1 killed	Shoemaker, 1919
1852	Elk Co., Ridgway on Clarion R.	7 of 12 killed by Indians from New York	Seton, 1929*c*
1853	McKean Co., near Teutonia	1 killed by S. Devens (see account for 1858, Potter Co.); specimen, ANSP 665	Murie, 1951
1853	Potter Co.	1 killed by J. Jordan; reported to be last killed in county	Beebe, 1934
1856	Potter Co.	1 killed; reported to be last killed in county	Swank, 1908
1857	Mifflin Co., Seven Mts. Treaster Valley	1 killed by C. Mitchell	Allen, 1942; Shoemaker, 1915*a*
1858	Potter Co., Cherry Springs	1 killed by S. Devens (see account for 1853 McKean Co.); specimen, ANSP 665	Murie, 1951
1858–1859	Tioga Co.	3 captured	Rhoads, 1903
About 1860	Lycoming Co., near Waterville on Little Pine Cr.	1 captured	Shoemaker, 1915*a*
1862	Elk Co.	1 killed (may be same as next record)	Seton, 1929*c*
1862	Elk Co., 25 mi from Driftwood, Hick's Run of Bennett's Branch of Sinnemahoning R.	1 killed by G. W. Gaylord and J. David	Rhoads, 1903
1862	Lycoming, Potter and Tioga cos., head of Pine Cr. and Black Forest	1 killed	Allen, 1942; Gerstell, 1936*a*; Rhoads, 1903
1862–1863	Potter Co.	1 killed by S. Wilcox	Rhoads, 1903

Table 12.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1863	Indiana Co., along Bear Run near Clearfield Co. line	1 killed by Jim Jacobs	Grimm and Roberts, 1950
1865	Clearfield Co.	1 killed by J. David	Allen, 1942; Shoemaker, 1915*a*
1865	Elk Co.	1 killed by Indians and purchased by J. David and W. Morrison	Rhoads, 1903
About 1865	Somerset Co., Laurel Hill	1 killed	Shoemaker, 1919
1866	Elk Co.	1 killed	Seton, 1929*c*
About 1866	Elk Co., Crooked Cr.	1 killed by Indians	Rhoads, 1903
1867	Elk Co., Flag Swamp, near Clarion R., and Bennett's Branch of the Susquehanna R. (near St. Mary's)	1 killed by Indian named J. Jacobs; reported to be last killed in state	New York Times, 19 Apr 1896; Era (Bradford) 12 Jan 1881; Allen, 1942; Decker, 1969; Gerstell, 1936*a*; Goodwin, 1936; McKnight, 1905*a*; Mohr, 1931; Murie, 1951; Rhoads, 1903; Seton, 1929*c*; Shoemaker, 1915*a*, 1919, 1929; Swank, 1908; Warren, 1867*a*
About 1869	Locality unknown	Indians from New York were reported to have killed a few elk and captured 1 calf	Harrisburg Daily Patriot, 16 Dec 1875
1869	Elk Co., near Ridgway	1 killed by S. Hunter	Shoemaker, 1915*a*
1869	Elk Co.	1 killed	Seton, 1929*c*
About 1870	Potter Co.	1 killed and reported by J. E. Cleveland	Rhoads, 1903
1872	Clinton Co., Grugan Twp.	1 killed by J. David	Shoemaker, 1929
1874	Elk Co.	1 reported killed; same individuals as 1830's for Warren Co.	Seton, 1929*c*
1875	Potter Co., near Roulette	1 killed by J. Jacobson; record discredited	Shoemaker, 1915*a*, 1919, 1929

Table 12.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1877	Centre Co., Decker Valley	1 killed by J. D. Decker	Shoemaker, 1919
1878	Locality unknown	2 killed	Allen, 1942; Shoemaker, 1939
1878	Union Co.; within 12 mi of Buffalo Cross Roads	1 killed; reported to be last killed in state	Faris, 1919
1881	Cambria Co., Black Lick Run	1 killed	Grimm and Roberts, 1950
	SPECIMEN RECORDS		
N.D.	Cumberland Co., Carlisle caves, near Carlisle	Skeletal parts	USNM 267551 and USNM 169721; U.S. National Museum of Natural History
1854	Potter Co.	Skull only; reported by Rhoads (1903) to be from McKean Co.	ANSP 665; Philadelphia Academy of Sciences
1973	Clearfield Co., Pottsdale	Jaw only; probably obtained from introduced stock (see text)	Pennsylvania State University

Indian named Jim Jacobs for killing the Commonwealth's last wapiti in Elk County in 1867. However, there is potentially some confusion about the incident, or incidents, involving Jim Jacobs. Grimm and Roberts (1950) reported Jim Jacobs killing one wapiti in 1863 in Indiana County. Shoemaker (1919) reports the same person also killing a wapiti in Clearfield County in 1865 and others elsewhere. Shoemaker (1919) also comments that Jacobs should not be confused with Jim Jacobson who supposedly killed a wapiti in 1867 in Elk County and others elsewhere until his last record in 1875 in Potter County (Allen, 1942; Shoemaker, 1915*a*). However, Shoemaker (1919) discredits the 1875 record. Regardless of the situations of wapiti killed by Jacobs or Jacobson, other authors (Decker, 1936; Goodwin, 1936; Mitchell, 1982) give credit to John D. Decker for killing the last wapiti in the Commonwealth which was in 1877 in Centre County. Based on chronology and geographical evidence (Fig. 12) this record is reasonable. However, unexpected reports of individuals killed in Cambria County in 1881, Indiana County in 1863 (Grimm and Roberts, 1950), and in Somerset

County about 1865 (Shoemaker, 1919) do not agree with chronology and geographical regression of the species. The extirpation of the species was primarily related to hunting pressure.

In 1913, an effort to reestablish *C. elaphus* in Pennsylvania was started. Fifty *C. e. nelsoni* were acquired from Yellowstone National Park and released in Clearfield and Clinton counties in equal numbers. Twenty-two additional wapiti were acquired from a private preserve in Monroe County, 12 of which were released in Monroe County and the remainder were released in Centre County. By the end of 1913, there was an accounted net loss of 12 individuals from the original 72 introduced wapiti. In 1915, an additional 95 wapiti were acquired from Yellowstone National Park and released (numbers in parentheses) in Blair (7), Cameron (24), Carbon (24), Forest (10), Monroe (6), and Potter (24) counties (Gerstell, 1936*a*). In 1924, six bulls were acquired from Wind Cave Game Preserve, South Dakota, and released in Elk County. Four more individuals were acquired from the same source in 1926, and released in the same county (Anon., 1936; Gerstell, 1936*a*).

Between 1923 and 1931, legal hunting of *C. elaphus* was permitted in Pennsylvania. During that time 98 wapiti were legally harvested, and another 78 were killed illegally or for damaging crops. Until the early 1970's, the Pennsylvania wapiti was not monitored and the population dropped to about two dozen individuals (Murie, 1951; Leffler, 1940). By the 1970's, the population was estimated to be 45 individuals. It is suspected that the brain worm *Parelaphostrongylus tenuis* (see account for white-tailed deer) was partially responsible for the decline of the introducted populations of *C. elaphus* (Mitchell, 1982). Through the efforts of the Pennsylvania Game Commission, Bureau of Forestry, and others, the population of wapiti in Pennsylvania has been investigated to ensure its survival (Eveland et al., 1979; Hassinger, 1981; Mitchell, 1982). In 1982, censuses revealed a population of 135 individuals in a 78-square-mile area of Cameron, Elk, and McKean counties—an area less than 75 miles from the last historical record of native wapiti in Pennsylvania. In previous years the population had been increasing an average of about 20% annually. However, the current population is now reaching numbers that are causing objectionable crop damage (Mitchell, 1982); therefore, further work is needed for managing the growing population.

Odocoileus virginianus—white-tailed deer

The white-tailed deer (*Odocoileus virginianus*) is also called the Virginia deer, white tail, and simply "deer" (Allen, 1942; DeKay, 1842; Rhoads, 1903). It is one of the most familiar and popular mammals in Pennsylvania. Doutt et al. (1973) reported that "about 2½ million . . . had been harvested by hunters . . ." since 1915. However, the white-tailed deer has been selected as a topic for discussion because of reports that the species was in danger of being extirpated in Pennsylvania between 1890 and 1910 (Allen, 1942; Doutt et al., 1973; Mohr, 1931; Rhoads, 1903; Shoemaker, 1919). O'Connor and Goodwin (1961) mention that there was a time when the "sight of a wild deer was a rarity," but stop short of stating that the species was near extirpation. Furthermore, it was also believed that the original large-sized subspecies (*Odocoileus virginianus borealis*) inhabiting Pennsylvania was replaced by a smaller subspecies (*O. v. virginianus*) from the south (Shoemaker, 1929). This account presents records that may help to separate fact from hearsay.

It is likely that the fluctuation in numbers of deer, either locally or throughout the Commonwealth, has been directly related to available habitat. Before the settlement of Pennsylvania, this species was relatively common as indicated by the proportionally larger quantities of skeletal remains found in archaeological and paleontological sites compared to other large-sized species. For example, at the Varner Site in Greene County (1200–1400 A.D.), 25% of all bone fragments were from *Odocoileus* (Guilday, 1961). The Eschelman Site in Lancaster County (1600–1625 A.D.) contained 17,118 fragments of deer bones (Guilday et al., 1962) and there were more than 609 *Odocoileus* bone fragments at the Johnston Site (1500–1600 A.D.) (Guilday, 1955). In the Carlisle caves, Cumberland County, the number of deer bones exceeded the total of all other mammalian remains in the caves (Miller, 1940).

Many of the historical records (Table 13) indicate that changes have occurred in both the deer population and forested areas since the colonization of Pennsylvania. Early records (Table 13) suggest that the deer was thought to be an inexhaustible resource as indicated by individual hunters killing as many as 100 deer in a single season (McKnight, 1905*a*). Table 13 also indicates that the species provided a livelihood for many residents of the Commonwealth throughout the nineteenth century. Furthermore, there was a desire to manage the deer population beginning as early as 1840 (Table 13). Records indicate that up until the mid-1800's, the deer population was still relatively stable.

The white-tailed deer is adaptable to a variety of habitats. However, it may be possible to threaten the stability of the population in areas where major changes occur over a short period of time. During the late 1800's and early 1900's, the impact of lumbering included short railroad lines for the removal of all qualities of timber for a wide variety of uses (Casler, 1973, 1976; Kline, 1970, 1971, 1975; Taber, 1970, 1971, 1972*a*, 1972*b*, 1974, 1975). This impact was so great in the Upper Allegheny River Basin (Clarion, Crawford, Erie, Forest, Venango, and Warren counties) that 225,279 acres of timber were removed

Table 13.—*Historical records of* Odocoileus virginianus *from Pennsylvania.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1682	Chester Co.	Venison sold for 2 shillings	Proud, 1797
1736–1823	Chester Co., near West Chester	S. Jefferies recalls when deer were plentiful in county	Watson, 1844
1740	"Lancaster Co."	Severe winter killed many deer	Pennsylvania Gazette, 9 Apr 1741
1745–1823	Philadelphia Co.	A. Johnson recalls that deer became scarce during his lifetime	Watson, 1844
1752	Northampton Co.	Formerly plentiful, now scarce	Proud, 1798
1760	"Lancaster Co." along what is now Downingtown to Harrisburg area	Plentiful	Ellis, F. and S. Evans, 1883
1769	Allegheny Valley	2000 deer killed during fall of 1769	de Schweinitz, 1887
1770	Chester Co., Corner Stores Village	"Last" 2 in county seen by M. Coastes children	Pennypacker, 1872
About 1775	Cambria Co., Kittanning Point	Extremely plentiful during Revolutionary War, only hindquarters eaten	Shoemaker, 1916
1798	Centre Co.	Philips Store received four times as many deer as any other wild animal	Row, 1909
1800–1805	Susquehanna Co.	J. Sabin killed at least 200 in four years	Blackman, 1873
1818–1858	Centre Co., vicinity of Snowshoe	Askey killed about 800 during his residence in area	Linn, 1883
1818	Bradford Co.	1000 men killed 150 deer on 4 Dec	Warren, 1897*b*
1830	Jefferson Co., on North Fork	Long killed 60 in one season	McKnight, 1905*a*
1831	Centre Co.	Considered scarce this season	Hazard, 1831*b*
1831	Mifflin Co., Lewistown	"Deer have never been as numerous as they are this season"	Hazard, 1831*b*
1832	Jefferson Co.	W. Long killed 165 during this season	Watson, 1844

Table 13.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1832	Northampton Co., vicinity Bethlehem	Locally extirpated	Lloyd, 1906
1833	Jefferson Co., Boone Mts.	W. Long killed 105, M. Long killed 104 in season	McKnight, 1905*a*
1840–1848	Luzerne Co.	J. McHenry killed 1900 in eight years	Pearce, 1866
1840	Monroe, Pike, Wayne cos.	Hunting banned	P. L. 117 Sec. 6
1850–1885	Throughout Commonwealth	Venison placed on free lunch counters in Pittsburgh and Philadelphia	Anon., 1970
1858	Northern and western counties of Commonwealth	Abundant, supplying venison to Baltimore and Philadelphia	Pennsylvania Telegraph, 14 Dec 1858
1858	Northumberland Co.	Extremely plentiful, shipped by rail daily to big cities	Pennsylvania Telegraph, 18 Dec 1858
1859	Dauphin Co.	Not plentiful, law bans hunting with dogs on 8 Apr	Pennsylvania Daily Telegraph, 8 Apr 1859
1860	Huntingdon Co.	Unusually abundant	Journal and American, 4 Jan 1860
1861–1865	Clinton Co.	Numerous, destroying crops	Warren, 1897*b*
1861	Clearfield Co.	Extremely numerous	The Patriot and Union, 30 Nov 1861
1861	Blair, Cambria, and Fayette cos.	Extremely numerous	Pennsylvania Daily Telegraph, 30 Nov 1861
1864	Huntingdon Co.	Unusually abundant	Daily Telegraph, 15 Dec 1864
1864	Blair Co.	Unusually abundant	True Democrat, 7 Dec 1864
1867	Forest Co.	Considered abundant	Patriot and Union, 3 Jan 1867
1867	Warren Co.	Considered abundant	Patriot and Union, 28 Jan 1867
1867	Lackawanna Co., Lehigh	Considered scarce	Record of the Times, 2 Oct 1867
1868	Fulton Co.	Abundant	Morning Patriot, 28 Dec 1868
1868	Clearfield Co.	H. Kelley killed 13 on 22 Dec	Greensburg Herald, 30 Dec 1868

Table 13.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1873	Clearfield Co.	41 shot by two men in one day	Harrisburg Daily State Journal, 6 Jan 1873
1873	Westmoreland Co., St. Clair Twp.	Over 100 killed in Dec in township	Clearfield Raftsman's Journal, 28 Jan 1874
1875	Throughout Commonwealth	Killing prohibited after 1 Dec	Huntingdon Journal, 26 Nov 1875
1875	Huntingdon Co.	Considered very scarce	Huntingdon Journal, 3 Dec 1875
1876	Throughout Commonwealth	Almost no deer being sent to cities by rail this year	Harrisburg Daily Patriot, 3 Nov 1876
1876	Cumberland Co., South Mt.	S. Spangler killed the only two known deer this winter	Carlisle Herald, 7 Dec 1876
1877	Dauphin Co.	Venison retails for 25 cents per pound	Harrisburg Daily Patriot, 16 Dec 1876
1877	Elk Co.	County ban on deer hunting for five years	Raftsman's Journal, 28 Mar 1877
1877	W. branch, Susquehanna R.	57 killed by hunting party	New Era, 30 Nov 1877
1877	Huntingdon Co.	Scarce	Huntingdon Journal, 30 Nov 1877
1877	Allegheny Mts.	Numerous deer killed this season	Huntingdon Journal, 14 Dec 1877
1878	Huntingdon Co.	Very few deer this season	Huntingdon Journal, 4 Jan 1878
1878	Clearfield Co.	"Lowest deer population in anyone's memory"	Huntingdon Journal, 18 Jan 1878
1878	York Co.	Considered very scarce	York Daily, 25 Nov 1878
1878	Pennsylvania	About one third the amount of deer being sent to cities as in previous years	Harrisburg Daily Patriot, 26 Nov 1878
1879	McKean Co., Bradford	Venison locally plentiful	Era, 10 Nov 1879
1879	Huntingdon Co.	Continue to be scarce	Huntingdon Journal, 12 Dec 1879
1879	Luzerne Co.	Plentiful	Weekly Telegraph, 19 Dec 1879
1880	Clearfield Co.	Not plentiful	Weekly Telegraph Post, 21 Oct 1880

Table 13.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1880	Franklin Co., near Greencastle	Deer seen—unusual occurrence	Shippensburg News, 17 Jan 1880
1880	Pike Co.	County residents make living by selling venison to city markets	Era, 7 Oct 1880
1880	Allegheny Mts.	Abundant	Harrisburg Telegraph, 10 Nov 1880
1880	Huntingdon Co.	Considered unusually plentiful	Huntingdon Globe, 25 Nov 1880
1880	Pike Co., Milford	Ban on deer hunting lifted, on 4 Oct., use of dogs still illegal, many hunters coming in from New York	Era, 7 Dec 1880
1880	Pike Co.	Considered more abundant than in last 25 years	Union Leader, 17 Dec 1880
1880	Elk Co.	Deer selling for 6 cents per pound	Harrisburg Telegraph, 21 Dec 1880
1881	Clearfield Co.	Unusually plentiful	Raftsman's Journal, 7 Dec 1881
1881	Westmoreland Co.	Abundant	Tribune Herald, 20 Dec 1881
1882	Franklin Co., near Carrick	Plentiful	Shippensburg News, 2 Dec 1882
1892–1893	Huntingdon Co., Diamond Valley	60 killed	Warren, 1897*b*
1892	Adams Co.	32 killed in ten mile radius	Rhoads, 1903
1895	Adams Co.	50 killed in ten mile radius	Rhoads, 1903
1896	Cumberland Co.	15 killed	Rhoads, 1903
1896	Huntingdon Co., Mt. Union	Deer found in this area	Rhoads, 1903
1897	Adams, Clearfield, Clinton, Elk, Franklin, Fulton, Huntingdon, Pike, Potter, and Tioga counties	Common	Warren, 1897*b*
1897	McKean Co., near Kane	Plentiful	Warren, 1897*b*
1897	Westmoreland Co., near Ninevah	Plentiful	Warren, 1897*b*

Table 13.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1897	Throughout Commonwealth	Salt licks prohibited for hunting deer	Anon., 1970
1897	Venango Co.	27 killed	Rhoads, 1903
1898	Carbon Co.	28 killed this season	Rhoads, 1903
1898	Clinton Co.	10–15 deer range over 3 square mile area	Rhoads, 1903
1898	Crawford Co.	None killed this season	Rhoads, 1903
1898	Elk Co.	Very scattered, 24 killed	Rhoads, 1903
1898–1899	Forest Co.	Deer numerous, 20 killed	Rhoads, 1903
1898	Mifflin Co.	8 killed	Rhoads, 1903
1898	Monroe Co., (northwest part)	4 killed	Rhoads, 1903
1898	Pike Co.	30 killed	Rhoads, 1903
1898	Potter Co.	Very few killed	Rhoads, 1903
1898	Somerset Co.	None known killed this year	Rhoads, 1903
1898	Union Co., Allegheny Mts.	Numbers increasing	Rhoads, 1903
1899	Luzerne Co. vicinity of North Mt.	5 taken into Pittston	Rhoads, 1903
1899	Lycoming Co., Loyalsock Cr.	Increasing since 1896	Rhoads, 1903
1899	Tioga Co.	Few left in county	Rhoads, 1903
1899	Westmoreland Co.	None killed for several years	Rhoads, 1903
1900	Centre Co.	Fairly abundant	Rhoads, 1903
1900	Clinton Co.	20 killed	Rhoads, 1903
1900	Columbia Co., Fish Cr., North Mt.	A few killed yearly	Rhoads, 1903
1900	Lackawanna Co.	Nearly extirpated	Rhoads, 1903
1900–1901	McKean Co., Colegrove	4 deer killed	Rhoads, 1903
1900	Sullivan Co.	"Rare," 6–8 killed this year	Rhoads, 1903
1900	Venango Co.	There are as many in county as there were 15 years ago	Rhoads, 1903
1900	Wyoming Co.	2 killed	Rhoads, 1903
1901	Cambria Co.	A few remain	Rhoads, 1903
1903	Wayne Co.	Very scarce	Rhoads, 1903
1905	Throughout Commonwealth	Buckshot banned for deer hunting	Anon., 1970
1906	Pennsylvania	50 deer stocked from Michigan	Anon., 1970
1907	Pennsylvania	Doe hunting banned	Anon., 1970

Table 13.—*Continued.*

Date	Locality	Comments	References
		HISTORICAL RECORDS	
1907	Forest Co., Jenkins Twp., Beavers Meadows	Only one killed in county this year	Titusville Herald, 5 Dec 1907
1917–1950	Pennsylvania	First camp limit established	Anon., 1970
1927	Cumberland and Lycoming cos.	139 and 46 antlerless deer killed, respectively, due to overabundance	Anon., 1970
1928	Lycoming Co. mountains	2000 deer killed during two week season, still plentiful	Anon., 1970
1931	Throughout Commonwealth	95,051 killed in first season on both doe and buck	Anon., 1970
1938	Throughout Commonwealth	First statewide antlerless season, 171,662 killed	Anon., 1970
1939	Throughout Commonwealth	Estimated deer population—825,000	Anon., 1940
1940	Throughout Commonwealth	All-time record harvest—186,575 killed in season	Anon., 1970
		SPECIMEN RECORDS (Records prior to 1925)	
About 1850	Tioga Co. near Wellsboro	Antlers only	CM 59942; Carnegie Museum of Natural History specimen
1895	Clinton Co., Round Island	Female, collected 14 Nov	ANSP 9614; Philadelphia Academy of Science specimen
1896	Clinton Co., Round Island	Female, collected 18 Aug	ANSP 9612; Philadelphia Academy of Science specimen
1915	Cameron Co.	Male, collected 4 Dec; skull preserved	CM 3227; Carnegie Museum of Natural History specimen
1915	Cameron Co.	Male, collected 4 Dec; skull preserved	CM 3228; Carnegie Museum of Natural History specimen
1915	Cameron Co.	Male, collected 11 Dec; skull preserved	CM 3229; Carnegie Museum of Natu-

Table 13.—*Continued.*

Date	Locality	Comments	References
SPECIMEN RECORDS (Records prior to 1925)			
			ral History specimen
1915	Elk Co., St. Mary's, Trout Run	Male, collected 8 Dec; skin, skull and body preserved	CM 3234; Carnegie Museum of Natural History specimen
1915	Elk Co., St. Mary's, Trout Run	Male, collected 7 Dec; skin and skull preserved	CM 3236; Carnegie Museum of Natural History specimen
1915	Elk Co., St. Mary's, Trout Run	Female; collected 7 Dec; skin, skull and body preserved	CM 3235; Carnegie Museum of Natural History specimen
1915	Elk Co., Tambine	Female, collected 9 Dec; complete skeleton preserved	CM 3237; Carnegie Museum of Natural History specimen
1922	Locality unknown	Male, collected 4 Dec; received from PA Game Commission; skin and skull preserved	CM 5315; Carnegie Museum of Natural History specimen
1922	Locality unknown	Male, collected 4 Dec; received from PA Game Commission; skeleton preserved	CM 5316; Carnegie Museum of Natural History specimen
1922	Clearfield Co., Penfield	Male, collected 4 Dec; received from PA Game Commission; skeleton preserved	CM 5317; Carnegie Museum of Natural History specimen

between 1896 and 1910 (Wilhelm, 1953) and Allen (1942) indicated that the deer had been extirpated from the region of those counties. As a result of similar logging practices throughout Pennsylvania, forests had reached an all time low of 12,000,000 acres by 1900 (Illick, 1923). This is the same time period that the deer population was considered to be at its lowest (Doutt et al., 1973). Rhoads (1903) reported that among 26 counties (Fig. 13), a small majority (15) reported a decline in the deer population. Even during this period Rhoads (1903) also indicated that the deer were abundant in some areas (Table 13).

Between 1906 and 1925, 668 deer were imported from Michigan, New Hampshire, New Jersey, Ohio, Maine, North Carolina, and Ken-

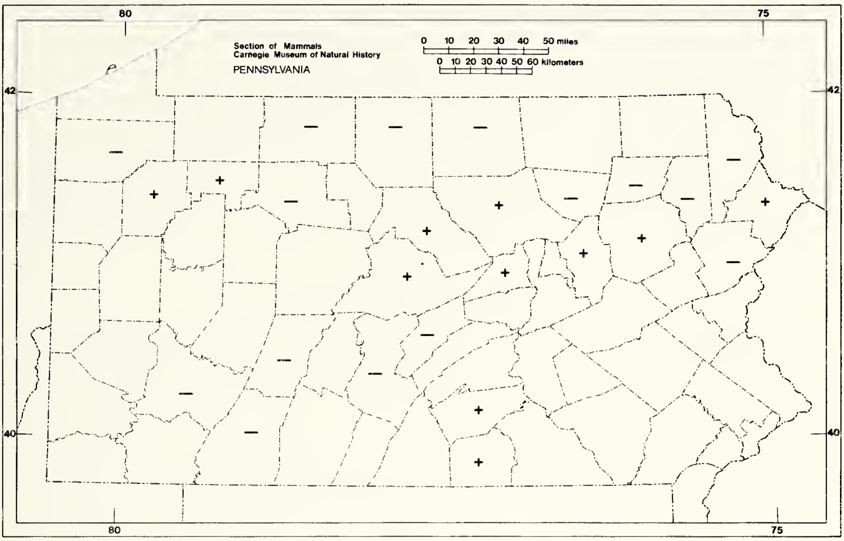
Section of Mammals
Carnegie Museum of Natural History
PENNSYLVANIA
0 10 20 30 40 50 miles
0 10 20 30 40 50 60 kilometers
80
75
42
40

Fig. 13.—Map of Pennsylvania showing relative abundance of *Odocoileus virginianus* during the 1890's, based on reports to Rhoads (1903). A "+" indicates reports of common occurrence and "−" represents reports of scarcity.

tucky by the Pennsylvania Game Commission. At the same time, 524 deer were being moved within the Commonwealth. Because Rhoads (1903) indicated that in some regions of the Commonwealth deer were common (Fig. 13; Table 13), it is unlikely that the original Pennsylvania deer population was affected by introductions or migrations from the south. The reports of smaller-sized deer can be explained as a variation of opinion, or by periodic poor environmental conditions that affect the physical appearance of individuals throughout a population (Forbes et al., 1971).

In 1931 over 95,000 deer were reported killed in the first open season held by the Game Commission (Anon., 1970). The deer population has continued to increase.

An interesting aspect of the biology of the white-tailed deer is the possible influence the brain worm parasite (*Parelaphostrongylus tenuis*) has had on the history of other mammals in Pennsylvania. Although the presence of the brain worm may affect the ability of the deer to cope with adverse conditions (Forbes et al., 1971), it has a greater effect on other cervids, such as *Alces alces* and *Cervus elaphus* (see accounts for moose and wapiti). The presence of one phase of the life cycle of this nematode was found in *Odocoileus virginianus* lung in 1945 (Dougherty, 1945). Later, DeGuisti (1955) found the adult worm within the meninges of white-tailed deer from Michigan. Alibasoglu et al. (1960) found that 75% of the deer examined from Pennsylvania harbored this parasite. In white-tailed deer, it is apparently tolerated, with first stage larval forms being expelled via the digestive tract. Later, the infective stage is picked up by any of a variety of both aquatic and terrestrial snails which serve as intermediate hosts (Karns, 1967). It is difficult to assess the past effect of this parasite on cervid populations in Pennsylvania. However, the importance of this nematode has been documented (DeGuisti, 1955; Mitchell, 1982).

Rangifer tarandus—caribou

The caribou is distributed throughout the northern hemisphere in arctic and subarctic regions where the proper vegetation and climatic conditions exist (O'Connor and Goodwin, 1961). In Europe and Asia, this animal is called the reindeer.

The primary evidence that *Rangifer tarandus* ever lived in Pennsylvania comes from at least two Pleistocene sites (Table 14; Fig. 14).

Table 14.—*Paleontological and historical records of* Rangifer tarandus *from Pennsylvania.*

Date	Locality	Comments	References
	PALEONTOLOGICAL RECORDS		
Pleistocene	Bucks Co., <1 mi S Riegelsville, Durham Cave	Possible caribou skeletal remains	Hay, 1923
Pleistocene	Monroe Co., 2½ mi SW Stroudsburg, Hartman Cave (=Crystal Hill Cave)	Jaws and teeth fragments found	Hay, 1923; Leidy, 1880, 1889; Rhoads, 1903
5688–8000 BC	York Co., Manchester Twp., ¼ mi E Emigsville, Bootlegger Sink	Skeletal remains of 1 individual; preserved specimen	Guilday et al., 1966
	HISTORICAL RECORD		
1850	Clinton Co., edge Tamarack Swamp	J. Hennessy found antlers of either moose or caribou	Shoemaker, 1912
	SPECIMEN RECORD		
5688–8000 BC	York Co., Manchester Twp., ¼ mi E Emigsville, Bootlegger Sink	Skeletal remains	CM 7986; Section of Vertebrate Fossils, Carnegie Museum of Natural History

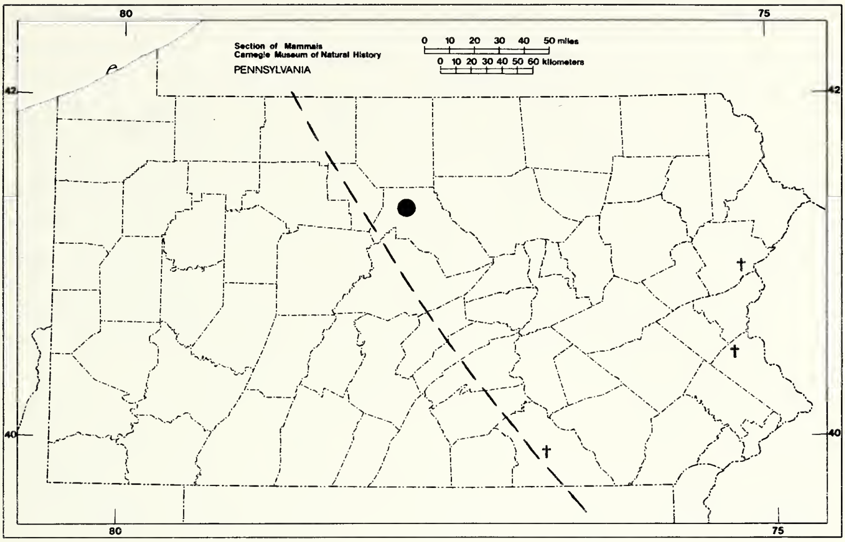
80
75
Section of Mammals
Carnegie Museum of Natural History
PENNSYLVANIA
0 10 20 30 40 50 miles
0 10 20 30 40 50 60 kilometers
42
40
80
75

Fig. 14.—Map of Pennsylvania showing location of records of *Rangifer tarandus*. Symbols used are described in Fig. 1.

Guilday et al. (1966) describe caribou remains found at Bootlegger Sink, York County. Guilday et al. (1966) also discussed the much earlier discovery of *Rangifer* jaws and teeth fragments at Hartman Cave (now called Crystal Hill Cave) in Monroe County (Leidy, 1880, 1889; Rhoads, 1903). Hay (1923) states that Leidy made reference to *Rangifer* remains at Durham Cave, Bucks County, in preliminary descriptions of faunal deposits at that site. However, Hay (1932) notes that in Leidy's (1889) subsequent report, *Rangifer* was not listed for Durham Cave. It may have been decided that the preliminary identification was incorrect. There were moose (*Alces alces*) remains listed in Leidy's (1889) report.

There are also Pleistocene sites containing caribou remains in several nearby states. An antler (Peabody Museum, Harvard University) was found at Trenton, Mercer County, New Jersey (Rhoads, 1903). Guilday (1969*b*) described seven pieces of caribou dating about 10,890 B.C. from the Dutchess Quarry Cave in Orange County, New York. In Saltville, Virginia, another late Pleistocene deposit was discovered containing *Rangifer* remains (Ray et al., 1967).

An antler of "either caribou or moose" was ploughed up by a Clinton County man near Tamarack Swamp in 1850 (Shoemaker, 1912). If this antler is from a Pennsylvania *Rangifer,* it is not likely that it is from Recent times.

There is no evidence to indicate that caribou have ever ventured as far south as Pennsylvania in historic times. There have been occasions during historic times when caribou have invaded Maine (Cahalane, 1947), Vermont, and New Hampshire (Hall, 1981). Overgrazing coupled with the damage caused by trampling (Cahalane, 1947) in the delicate substrate of the tundra can have a serious impact for an extended period of time. Cahalane (1947) points out that caribou cannot continuously follow the same migration routes because of the inability of the environment to sustain such repeated assaults. However, seasonal movement is exhibited by the various North American subspecies and is characterized by a change in diet and snow conditions (Banfield, 1974). Food shortages may explain these sporadic ventures into the southern limits of the known range (Cahalane, 1947).

During the Pleistocene, suitable food and climate for the caribou were more widespread. Evidence of the corresponding range of the caribou has been found in numerous Pleistocene Holarctic deposits. At the beginning of the post-glacial Holocene *Rangifer* populations followed the northward recession of the ice (Kendeigh, 1974).

***Bison bison*—bison**

The existence of *Bison bison* in Pensylvania has been reported by numerous authors (Allen, 1942; Allen, 1876; Garretson, 1938; Goodwin, 1936; Hornaday, 1889; Rhoads, 1903; Seton, 1929*d*; Shoemaker, 1913, 1915, 1919, 1929, 1944, 1948*b*; Walker, 1958). Garretson (1938) remarks, "There is ample proof that bison were found in considerable numbers on the eastern slope of the Alleghany Mountains and that they were gradually extending their range eastward and southward." In 1760, 111 bison were reported to have been taken in a "roundup" in Snyder County (Gerstell, 1936*a*). Rhoads (1903) states that *Bison* were ". . . found in the valleys and mountain glades of the Ohio, Monongahela and Allegheny Rivers, whence it passed sparingly eastward across the Allegheny passes into the tributary valleys of the Susquehanna . . . ."

Guilday (1963) and a review of the literature reveal many of the stories of *Bison* in Pennsylvania originated with an early account given in *Travels in America in 1806* by Thomas Ashe. In this account, behavior, migrations, hunting, numbers exceeding ten thousand, and even the destruction of a log cabin were reported. Subsequently, these stories were perpetuated, often verbatim, by other authors (Allen, 1942; Allen, 1876; Garretson, 1938; Hornaday, 1889; Rhoads, 1903; Shoemaker, 1915, 1919; Walker, 1958). With regard to the popular reference to accounts by Ashe, Guilday (1963) raises questions about the geographic locality as well as the authenticity of the accounts. Guilday (1963) remarks that "Ashe was a blatantly anti-American Englishman who wrote for the benefit of his English public, and some of his accounts are, to say the least, quite colorful." Guilday (1963) concludes, "In view of the vagueness of the locality and the known propensity of Thomas Ashe for colorful embellishment without regard for fact, this oft-quoted account cannot be considered seriously."

Although Thomas Ashe's accounts may be questionable, there are additional reports to suggest *Bison* occurred in Pennsylvania. Shoemaker (1915) not only supported the occurrence of *Bison* in the Commonwealth, but he considered it unique from western populations, thus giving it the name *Bison americanus pennsylvanicus.* Because Shoemaker's (1915) description was based on hearsay from descendants of early settlers that supposedly hunted bison in Pennsylvania, the name *B. a. pennsylvanicus* was considered invalid (Hall, 1981; according to Opinion 2 of the International Commission on Zoological Nomenclature ". . . a *name* . . . refers to the designation by which the actual objects are known . . . . Names based upon hypothetical forms have, therefore, no status in nomenclature and are not in any way entitled to consideration under the law of priority."—Stiles, 1907). Furthermore, Schorger (1944) presents information to suggest that the bison in Pennsylvania did not actually differ that much from western populations.

Other reports of bison involve specific accounts of killing the last individuals in Pennsylvania (Table 15). These accounts have been perpetuated as much as those accounts of Ashe, but with some inconsistencies. For instance, there is some controversey over the last bison killed in Pennsylvania. Traditionally, Col. John Kelley is credited for killing the last bison in 1801 in Union County (Walker, 1958; Shoemaker, 1913, 1915; Doutt et al., 1973; Garretson, 1938; Rhoads, 1897, 1903). However, Rhoads (1903) reported the date as "about 1790 or 1800." Others reported that in 1810 Frederick Stamm killed one bison in Northumberland County and Joseph Shank killed another in Somerset County (Anon., 1945; Goodwin, 1936; Mohr, 1931; Seton, 1929*d*; Shoemaker, 1929). Shoemaker (1919, 1944) reported John Yutsey as being the one who killed the individual from Somerset County (near Shanksville) in 1810 (Table 15). The inconsistencies (Table 15) between Shoemaker's (1913, 1915, 1919, 1929, 1944) publications are not understood. Perhaps these inconsistencies support Guilday's (1963) remarks of Shoemaker's writings as being "embellished folklore and hearsay uncritically presented."

In spite of the limitations of the historical records, it would seem that other evidence for the existence of the bison in Pennsylvania would be available. Some authors have given credit to names of geographical sites. However, Gibson (1969) discusses how many of these names were derived and were erroneously assumed to indicate the previous

Table 15.—*Paleo-archaeological, historical, and specimen records of* Bison bison *from Pennsylvania.*

Date	Locality	Comments	References
	PALEO-ARCHAEOLOGICAL RECORDS		
Recent	Cumberland Co., near Carlisle, Carlisle caves	Baird reports finding skeletal remains; not reported in subsequent work by Miller (1940)	Miller, 1940; Rhoads, 1903
N.D.	Fayette Co., 4 mi S Somerfield, Henry Clay Twp., Martin Site (36Fa23)	Four skeletal fragments; identification later questioned	Gilmore, 1946; Guilday, 1963
N.D.	Luzerne Co., Pittston	Two molars identified by J. Leidy of Philadelphia Academy of Sciences	Grimm and Whitebread, 1952; Rhoads, 1903
Quaternary	Monroe Co., 2½ mi SW Stroudsburg, Hartman's Cave, (=Crystal Hill Cave)	Leidy (1889) reports fragment of mandible with one damaged molar	Grimm and Whitebread, 1952; Leidy, 1889; Rhoads, 1903
Pleistocene	Montgomery Co. on Schuylkill R., below Valley Forge, Port Kennedy Cave	Bones from Cope's studies identified as being *Bison*; identification later questioned	Cope, 1871, 1899; Kurtên and Anderson, 1980; Rhoads, 1903
	HISTORICAL RECORDS		
N.D.	Mercer Co.	1 horn found in 1795–1797	Rhoads, 1903
1773	Locality unknown	P. Quigley estimated 12,000 existing in Pennsylvania	Anon., 1945; Rhoads, 1903; Seton, 1929*d*; Shoemaker, 1919; Walker, 1958
1792	Dauphin Co., Harrisburg, Maclay's Swamp	1 individual killed by community	Shoemaker, 1919, 1944, 1948*b*; Walker, 1958
1795	Mercer Co.	1 horn found according to B. S. Stokley	Rhoads, 1903
1798–1799	Clinton Co.	1 killed; reported to be last killed in county	Shoemaker, 1929
1799	Union Co., White Mts., Bonestiels Sink, near Weikert	Last herd slaughtered in snow drifts	Allen, 1942; Anon., 1945; Garretson, 1938; Seton, 1929*d*; Shoemaker, 1913, 1915*b*, 1919, 1929, 1944; Walker, 1958
1800	Cambria Co., Stony Cr.	1 killed by Capt. R. McGuire	Grimm and Roberts, 1950

Table 15.—*Continued.*

Date	Locality	Comments	References
	HISTORICAL RECORDS		
1800	Union Co.	Male, female, and calf observed by M. McClester; the calf was killed	Garretson, 1938; Shoemaker, 1915*b*
1801	Fayette Co., Laurel Hill section	1 killed by Laughlin	Grimm and Roberts, 1950
1801	Union Co., McClister Farm about 5 mi from Lewisburg	1 killed by Col. J. Kelley; traditionally accepted as last record for Pennsylvania	Allen, 1876; Anon., 1945; Doutt et al., 1973; Faris, 1919; Garretson, 1938; Mohr, 1931; Rhoads, 1897, 1903; Seton, 1929*d*; Shoemaker, 1913, 1915*b*, 1919, 1929, 1944; Walker, 1958
1802	Westmoreland Co., Indian Cr.	1 killed by Hufnagle	Grimm and Roberts, 1950
1805	Indiana Co., Montgomery Twp.	1 killed by M. Chambers	Grimm and Roberts, 1950
1808	Union Co., Buffalo Valley, Narrow Point	1 observed by J. Weikert	Anon., 1945; Mohr, 1931; Seton, 1929*d*; Shoemaker, 1929, 1944
1810	Northumberland Co., (now Union Co., Shoemaker, 1944)	1 killed by F. Stamm	Anon., 1945; Mohr, 1931; Seton, 1929*d*; Shoemaker, 1919, 1929, 1944
1810	Somerset Co.	1 killed by J. Shank	Anon., 1945; Goodwin, 1936; Mohr, 1931; Seton, 1929*d*; Shoemaker, 1929
1810	Somerset Co., near Shanksville	1 killed by J. Yutsey	Grimm and Roberts, 1950; Shoemaker, 1919, 1944
	SPECIMEN RECORD		
1932	Lehigh Co., Trexler Game Preserve, near Allentown	Skull; obtained from introduced specimens (see text)	ANSP 17772 and ANSP 17774; Philadelphia Academy of Sciences; Garretson, 1932

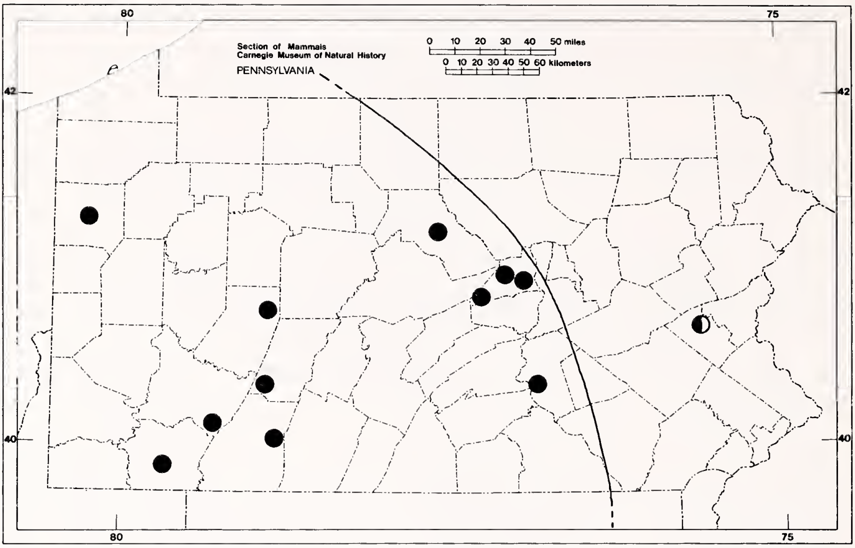
80
75
42
40
Section of Mammals
Carnegie Museum of Natural History
PENNSYLVANIA
0 10 20 30 40 50 miles
0 10 20 30 40 50 60 kilometers

Fig. 15.—Map of Pennsylvania showing location of historic records and possible distribution of *Bison bison*. There is some controversy as to whether the bison ever inhabited Pennsylvania (see text). The record from Lehigh County represents the Trexler herd which was introduced in 1911 and 1914. Symbols used are described in Fig. 1.

occurrence of bison. Also, it would seem that if large numbers of bison were killed, skeletal remains would be found. The absence of such remains may be partially explained by the fact that bones of bison were often collected for making fertilizer (Allen, 1942). Even anthropological and paleontological sites do not provide much evidence of bison ever inhabiting Pennsylvania. The few reports of skeletal remains have been subsequently questioned (Guilday, 1963; Kurtén and Anderson, 1980; Rhoads, 1903) or are not available for verification. Guilday (1971*b*) discusses the absence of bison remains from archaeological sites in the Ohio River valley. Perhaps the most supporting evidence of bison ever occurring in Pennsylvania are records from New York, Ohio, Maryland, and the Carolinas (Guilday, 1963).

In conclusion, there is no solid evidence to support the occurrence of bison in Pennsylvaina (Allen, 1942; Gibson, 1969; Guilday, 1963, 1971*b*; Hornaday, 1889). However, the abundance of traditional stories and surrounding paleo-archaeological records indicate that it probably did occur in the Commonwealth. It is likely that it never was present in great numbers (Guilday, 1963) as was suggested by early accounts.

In 1909, H. C. Trexler established a 3000-acre game preserve for bison in Lehigh County, 10 miles northwest of Allentown. In 1911, he added a pair of bison to the preserve and another pair in 1914. These bison (*B. b. bison*) originated from the Corbin herd near Newport, New Hampshire, which in turn originated from the Jones herd. The Jones herd included wild buffalo from the Texas panhandle as well as individuals purchased from owners in Kansas, Nebraska, and California. The Trexler herd had increased to 70 individuals in 1933. Four specimens from the Trexler herd were donated to the Philadelphia Academy of Sciences for public display (Garretson, 1938). Apparently skulls of two of these specimens were deposited in the mammal research collection at that institution.

CONCLUSIONS

It is believed that most of the primary publications and many obscure and otherwise unknown sources of information have been consulted. One of the major problems of conducting such a study is the difficulty in separating fact from folklore. Specific cases of questionable accounts have been discussed in the text. Folklore has been included in this review, because it has become a distinct part of the history of some species. It is interesting to note that wherever cases of folklore may exist, the chronology and geographical locations are often in general agreement with what is known about the historical records and more factual accounts of the species in question.

This study included recent reports of several species which are important and of interest to the scientific community. Although isolated reports may be viewed by some with skepticism, when such reports are grouped and plotted, a logical pattern often develops. Thus, we encourage responsible reporting of the occurrence of rare native species, whether it be by the scientific community or general public. Species of particular interest include *Martes americana, Martes pennanti, Taxidea taxus,* and *Felis concolor.*

This study has shown the ecological importance of the relationships within the entire biological community. The most obvious factor in the history of Pennsylvania was the effect of altering natural habitats. Species, such as the marten, fisher, lynx, and deer, may have been affected by the alteration of forested areas. The reduction of species, such as deer and elk, may have influenced the existence of predator populations. The extirpation of the wolf and the mountain lion undoubtedly had a counter effect on the deer at a later date. A similar predator-prey relationship exists between the lynx and snowshoe hare. Habitat alteration and predator-prey relationships are more obvious than other equally important factors, such as the subtle parasite-host relationships of the brainworm, deer, and other cervids. In this situation the survival of the moose and wapiti was affected by the interrelationships of the parasite, deer, and available habitat. The adaptability and fecundity of the deer allow it to survive under many conditions (Chapman and Feldhamer, 1982). However, other species have more stringent environmental requirements which may contribute to their extirpation. During the past century the deer has benefited from management and enumerable studies (Chapman and Feldhamer, 1982) that provided a more complete knowledge of the species. However, it is evident that to properly manage even a single species, a better understanding of the entire biological community is necessary. Additional studies are needed for other species. Such work will not only provide more information of subtle factors, such as parasite-host relationships, but would possibly expose relationships that are not currently known.

Although this study represents a conglomeration of many sources of information, it becomes apparent that the results of such an effort may provide an insight to the distribution and history of some species of Pennsylvania mammals. It is realized that the diversity of records ranges from possible folklore to preserved research specimens, but when the species is gone, that is about the only thing that remains.

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AMPHIBIANS AND REPTILES OF THE SESSÉ & MOCIÑO EXPEDITION: A LOST CHAPTER IN MEXICAN HERPETOLOGY

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Abstract

The botanical and zoological illustrations prepared during the Royal Botanical Expedition to New Spain (the Sessé and Mociño Expedition, 1788–1803) are in the collection of the Hunt Institute for Botanical Documentation, Carnegie-Mellon University. There are seven plates of amphibians and reptiles, six of them identifiable as Mexican species: *Ambystoma* sp., *Barisia imbricata, Phrynosoma* sp., *Phrynosoma asio, Ctenosaura hemilopha, Pseudoeurycea bellii.* Although these illustrations reached Europe before all but one of the species represented was known to science, none was described by contemporary herpetologists.

Herpetology of the Sessé & Mociño Expedition

The Royal Botanical Expedition to New Spain (better known as the Sessé & Mociño Expedition) was authorized by King Carlos III in 1786,

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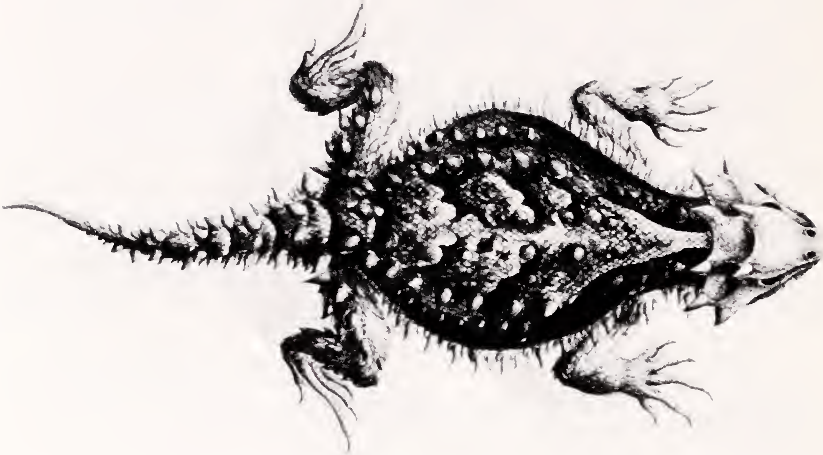

Fig. 1.—*Phrynosoma asio* (catalogue number 1258).

and began work in México in 1788. Credit for conceiving the idea of a botanical exploration of New Spain is usually given to Martín de Sessé y Lacasta (1751–1808), a Spaniard who served as administrative head of the Expedition throughout its 16 years of exploration in the New World. The principal botanist of the Expedition was José Mariano Mociño (1757–1820), who ultimately was the most productive scientist connected with the Expedition. Most of the zoological work of the Expedition was done by José Longinos Martínez (1750–1802), who made several independent trips to the Pacific Coast and Baja California. The zoological collections made by Longinos Martínez eventually formed the nucleus for the National Museum of Natural History of Mexico (Beltrán, 1982:66). Between 1788 and 1803, when surviving members of the Expedition returned to Spain, explorations and collections were made in the Caribbean, northern Central America, California, and as far north as Vancouver Island, although the great bulk of the collections and illustrations were made in México.

Throughout the Expedition skilled illustrators accompanied the collectors in the field, and made sketches from freshly-collected material. These sketches were subsequently rendered into the minutely detailed and exacting finished illustrations. After the termination of the Expedition and his return to Spain, Mociño worked for several years on the collections and illustrations. But the major results of the Expedition—

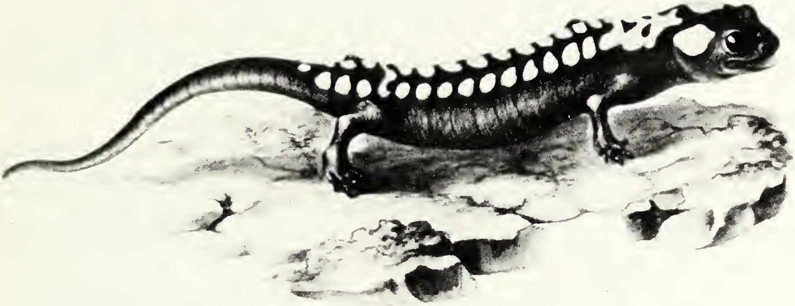

Fig. 2.—*Pseudoeurycea bellii* (catalogue number 1260).

Plantae Novae Hispaniae (Sessé and Mociño, 1887–1891), and *Flora Mexicana* (Sessé and Mociño, 1891–1897)—were not published until almost a century after the Expedition ended. After the death of Mociño in 1820 the original set of illustrations was dispersed with his property, and lost. The history of the Expedition and its personnel, the routes travelled and collecting localities, have been reviewed by Rickett (1947), Beltrán (1967), and McVaugh (1977).

Students of the flora and fauna of tropical America, and those interested in the history of exploration of the New World, now have a rich new resource available with rediscovery of the original illustrations. The lost Mociño collection of illustrations was acquired by the Torner family of Barcelona in the 1880's and preserved in their private library, but was not recognized as the missing illustrations from the Sessé & Mociño Expedition. The collection now resides in the Hunt Institute for Botanical Documentation, Carnegie-Mellon University, where it is known as the "Torner Collection of Sessé and Mociño Biological Illustrations." The history of the collection and the story of its rediscovery were related by McVaugh (1982).

Most of the illustrations in the collection, in keeping with the primary mission of the Expedition, are of plants. But approximately 200 of the plates represent animals of various taxonomic groups, including seven of amphibians and reptiles. Of these seven, six are identifiable as Mexican species, as follows (numbers refer to the catalogue of the collection in the Hunt Institute for Botanical Documentation):

Ambystoma sp. (1253).—This is a watercolor illustration of a large, neotenic larva, the famous "axolotl," in dorsal view. The ground color is gray to black, with fine black stippling, suggesting that the species depicted is *A. mexicanum,* or a closely related form.

Barisia imbricata (1254).—A large adult male with swollen temporal regions is posed on a branch in this watercolor illustration. The body, shown in lateral view, is greenish with the characteristic whitish flecks. The color shades to warm brown on the regenerated tail.

Phrynosoma sp. (1257).—This color illustration, showing both dorsal and ventral views on one plate, cannot be identified to species with certainty. The combination of characters depicted suggests that this drawing is either a composite taken from several different species, or an illustration drawn from memory.

Phrynosoma asio (1258).—This ink drawing of an adult specimen of *P. asio* shown in dorsal view (Fig. 1) is one of the most finely detailed and technically accurate in the collection.

Ctenosaura hemilopha (1259).—This excellent illustration of a subadult *C. hemilopha,* accurate in scale characters, color, and pattern, has been published (Anon., 1981).

Pseudoeurycea bellii (1260).—This watercolor illustration of a widespread Mexican species (Fig. 2) is accurate in color and morphological detail, but the awkward pose suggests that the artist did not see the living animal. From the geographically variable characters illustrated, the specimen probably originated from a population on the southern part of the Mexican Plateau, perhaps from Michoacán (D. B. Wake, personal communication).

DISCUSSION

The botanical illustrations in the rediscovered Torner Collection are expected to have a significant effect on botanical nomenclature and typification. Hundreds of new species of plants described by A. P. de Candolle and others were based on the illustrations as type-specimens (McVaugh, 1982). The zoological illustrations, in contrast, seem not to have reached the hands of scientists. The illustrations of amphibians and reptiles, which were vastly superior to the usual biological illustrations of the day, certainly depict their subjects in diagnostic detail. But even though the illustrations reached Europe at the beginning of the great era of descriptive biology, and before all but one of the illustrated species (*Ambystoma mexicanum*) were known to science, the amphibians and reptiles from the Sessé & Mociño Expedition were then, and remain today a lost chapter in Mexican herpetology.

RESUMEN

Con el reciente descubrimiento de las ilustraciones hechas durante la Real Expedición Botánica a la Nueva España (Expedición de Sessé y Mociño), se abren nuevas oportunidades para los interesados en el estudio de las ciencias naturales en el Nuevo Mundo.

La coleccion de casi 2000 dibujos, ahora conocida como Colección Torner, esta depositada en el "Hunt Institute" para la documentacion botánica. Se hace una breve reseña de la Expedición y sus integrantes. Se determinan 6 de las 7 ilustraciones de anfibios y reptiles como especies pertenecientes a la fauna de México, las cuales fueron conocidas por estos investigadores antes de llegar a los grandes museos Europeos.

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ECOLOGY, POSTNATAL DEVELOPMENT, MORPHOMETRICS, AND TAXONOMIC STATUS OF THE SHORT-TAILED OPOSSUM, *MONODELPHIS DIMIDIATA*, AN APPARENTLY SEMELPAROUS ANNUAL MARSUPIAL

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Abstract

Field data for *Monodelphis dimidiata* were collected from trapping sites near Balcarce, Buenos Aires Province, Argentina. Fallow pastures and native grasslands were live-trapped and snap-trapped as part of a rodent population dynamics study, extending from December 1968 to April 1970. The opossums represented only several percent of the total small mammal community captured each month. The greatest number were captured in the autumn (March--May), coinciding with the dispersal of the young. The animals were diurnal, with most of the activity concentrated in the late afternoon. Rarely were the opossums captured more than once. The species appears to be predominately

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insectivorous; it is not believed to be a major predator of rodents. Litters were documented for two summer months (December–January), with a high of 16 young recorded for one litter. Data on postnatal development were recorded for a limited number of young during the first five weeks after birth, close to the time of eye opening. Morphometric data from lab and field animals, and skull measurements show that the young developed rather slowly through the cooler months, whereas spring growth, especially in the males, increased drastically, with sexual maturation occurring in both sexes by summer.

Monodelphis dimidiata is shown to be an apparently semelparous and annual species. Temporal distribution of age group classes and patterns of non-geographic variation provide the primary support for this conclusion. In keeping with its apparent reproductive strategy, *M. dimidiata* shows extreme sexual dimorphism. Non-geographic variation is documented. The differences between the sexes in *M. dimidiata* and certain other *Monodelphis* have sometimes resulted in taxonomic problems, noted herein. Previously confounded with *M. henseli* (probably = *M. sorex*), *M. dimidiata* seems to be known with certainty only from Argentina and Uruguay. Although sometimes regarded as conspecific with *M. fosteri,* conspecificity has not been demonstrated.

INTRODUCTION

The New World marsupial genus *Monodelphis* Burnett contains from 14 to 18 species (genus under revision by Handley and Pine) and occurs from eastern Panamá to Argentina. Habitats range from tropical rain forest to xeric grassland. Except for *M. domestica* (Streilein, 1982*a,* 1982*b*), little else is known concerning these small, terrestrial, pouchless opossums.

Animals identified as *Monodelphis dimidiata* (Wagner) have been reported from southern Brazil, Paraguay, Uruguay, and much of the grassland of Argentina (Bertoni, 1939; Cabrera, 1958; Reig, 1964). Although several authors have contributed anecdotal notes on its natural history, only Reig (1964, 1965) added substantially to our knowledge of the species. Our report covers several aspects of the natural history, non-geographic variation, and the taxonomic history of *M. dimidiata.*

METHODS AND MATERIALS

A study area was located in the grasslands near Balcarce, Buenos Aires Province, Argentina. Dalby (1975) described the area and trapping procedures.

Over 30,000 trap nights were tallied in the Balcarce area in a period extending from December 1968 to April 1970. Sherman live traps (75 by 75 by 227 mm) were placed on two 1.2 hectare grids (10 by 10 with 12 m trap spacing). One grid was in a fallow pasture and the other was on a slope covered with native grasses. Each study plot was trapped for a three-day period every other week. Adjacent to the large grid in the fallow pasture was a smaller one (0.70 hectares, 7 by 7, 12 m spacing) which was live-trapped every three hrs, day and night, for three days (72 hrs), once a month for 13 months to determine activity patterns for small mammals. Roadside ditches were also trapped with live traps or with Museum Special snap traps in conjunction with another study. It was only in the last habitat that *Monodelphis* could be captured with any regularity, generally where the grasses and associated forbs were dense. Other areas containing *Monodelphis* *dimidiata* were described by Reig (1964), Fornes and Massoia (1965), and Massoia and Fornes (1967).

Some short-tailed opossums were maintained in captivity for various periods of time. They were housed in solid-bottomed rodent cages (ca. 30 by 30 by 50 cm), provided with wood shavings, and fed mainly bird and mammal road kills and snap-trapped mice. Water was provided *ad libitum.* These captives provided the opportunity to record data on growth and postnatal development.

Skins and skulls representing 41 wild-caught individuals and deposited in The Museum, Michigan State University, were used in the analysis of non-geographic variation. These specimens from the Balcarce area were assigned to six relative age classes somewhat similar to those described by Gardner (1973) for *Didelphis.* We had no specimen of Gardner's "age class 1" (M2 not completely erupted). Our age classes were as follows: age class 2, M2 and m2 in position, M3 and m4 may be erupting but are not in position; age class 3, M3 in position and milk (deciduous) premolars not being replaced; age class 4, m4 in position, permanent PM3 erupted but not fully in place; age class 5, all permanent teeth erupted but M4 with little or no wear; age class 6, M4 with moderate wear, m4 with little or no wear; age class 7, M4 with heavy wear, m4 with moderate to heavy wear. Data from captives were pooled with those from animals killed when trapped.

External measurements were taken in the field and laboratory according to the North American system (ear to notch, hind foot including claw). All skull measurements were taken with dial calipers reading to the nearest twentieth of a millimeter. Some of the skull measurements correspond to those used by Tate (1933) for *Marmosa* and by Gardner (1973) for *Didelphis.* Measurements of toothrows and mandibles were taken on the left side except when correct measurements were attainable only on the right side. The measurements were:

Skull length.—The greatest linear measurement attainable.

Condyloincisive length.—From the anteriormost projection of the incisors to a line through the posteriormost projections of the occipital condyles.

Palatal length.—From the anteriormost projection of the incisors to the posteriormost point on the midline of the palate.

Greatest nasal length.—Greatest length of the longer nasal.

Zygomatic breadth.—Greatest dimension from the outside (lateral) edge of one zygomatic arch to that of the other—a measurement perpendicular to the sagittal plane of the skull.

Postzygomatic braincase width.—Least width of skull taken posterior to posterior roots of zygomatic arches and anterior to lateral expansion of lambdoidal crests.

M3–M3.—The greatest distance between the most lateral point on the right upper third molar and the corresponding point on the left upper third molar.

Maxillary toothrow.—From the anteriormost projection of an upper canine to the posteriormost projection of the fourth upper molar on the same side of the skull.

M1–M4.—From the anteriormost point on the first upper molar to the posteriormost point on the fourth upper molar on the same side of the skull.

Postorbital constriction.—Least distance between lines perpendicular to horizontal planes of skull and which touch the lateral margins of the skull in the postorbital region posterior to the lateral expansions of the frontals.

Mandibular depth.—Depth of mandibular ramus immediately behind the fourth lower molar.

Length of ramus.—Distance between anteriormost projection of first lower incisor and the posteriormost point on the mandibular condyle of ramus bearing that tooth.

Mandibular toothrow.—From anteriormost point on first lower incisor to posteriormost point on fourth lower molar (both points on teeth of a single mandibular ramus).

Specimens examined (USNM = National Museum of Natural History, Smithsonian Institution; MSU = The Museum, Michigan State University; FMNH = Field Museum of Natural History).—MONODELPHIS HENSELI [probably = *M. sorex* according to Handley (personal communication)]. *Brazil*: Minas Gerais: Passos (20°43′S, 46°37′W), 428 m, 1 ♂ (USNM 304594). Rio de Janeiro: "Campo Bello" = Itatiaya (=Itatiaia at 22°30′S, 44°34′W), 1 ♂ (USNM 461068—the holotype of *P*[*eramys*]. *d*[*imidiata*]. *itatiayae* A. de Miranda-Ribeiro). São Paulo: Boracéia: Casa Grande, *ca.* 20 k S Salesópolis (the last is at 23°32′S, 45°51′W), 1 ♂ (USNM 460504). São Paulo: Ribeirão da Lagoa (also *ca.* 20 k S Salesópolis), 1 ♂ (USNM 484016). MONODELPHIS DIMIDIATA. *Argentina*: Buenos Aires Prov.: Partido Balcarce: Estación Experimental del Instituto Nacional de Technología Agropecuaria (INTA), *ca.* 15 k NW Balcarce (Balcarce at 37°51′S, 58°16′W) and nearby, *ca.* 100–150 m: "INTA," 4 sex? (MSU 20247–20250); "INTA/ditch near buildings," 1 ♀ (MSU 17675); "INTA property in overgrown pasture," 1 ♀ (MSU 17586); "INTA, in ditch (grass tall) near buildings," 1 ♂ (MSU 17674); "INTA area, Ruta 226, ditch," 5 ♂♂ (MSU 18520–18522, 18524, 18525); "Ruta 226 ditch, 1 km west of INTA gate," 1 ♂ (MSU 18262); "near INTA, Ruta 226, Km 74, ditch," 1 ♂, 2 ♀♀ (MSU 18339, 19182, 19193); "roadside trapping near INTA entrance," 1 ♂ (MSU 17887); "Ruta 226 ditch, Km 74," 1 ♀ (MSU 18699); "ditch along INTA side along Ruta 226 Km 68," 1 ♂ (MSU 18789); "in ditch along Ruta 226, approx. Km 78," 1 ♀ (MSU 18691); "ditches along Ruta 226 between Km 65–75," 2 ♂♂, 2 ♀♀ (MSU 19227–19230); "ditch along Ruta 226," 3 ♀♀ (MSU 18579, 18698, 18699); "Hill Plot," 150 m, 1 ♀ (MSU 19834); Prov. Buenos Aires: Partido Balcarce, "Crovetto Field," *ca.* 6 k N Balcarce (Balcarce at 37°51′S, 58°16′W), 100 m, 6 ♂♂, 6 ♀♀, 1 sex? (MSU 17469, 17470, 17599, 17641, 18573, 18652, 18781, 19317, 19335, 19596, 19697, 19699, 20036); Pergamino (33°53′S, 60°36′W), Ruta 188, Curva de Peña, 1 ♀ (FMNH uncataloged).

Natural History

Ecology and Behavior

Knowledge of *M. dimidiata* is limited, in part because the species seems to occur at low densities. Snap-trapping in a nearby *partido* (county) over a number of months in 1963 and 1964, and in a number of habitats, Reig (1965) noted that of 550 animals trapped, slightly less than 6% consisted of this species, a result comparable to ours. Of 32 (17 ♂♂, 15 ♀♀) individuals trapped from December 1968 through all of 1969, the greatest number were captured in the autumn (March–May), coinciding with the dispersal of the young. Breaking down captures by month gives: *Summers* (complete summer of 1968–69 plus December of 1969), 5 + 4 (December 1968, 3; January, 1; February, 1; December 1969, 4—one study plot designated "Activity Plot" not in operation during these times); *Autumn* of 1969, 19 (March, 7; April, 5; May, 7); *Winter* of 1969, 6 (June, 3; July, 0; August, 3); *Spring* of 1969, 9 (September, 0; October, 1; November, 8). Because some animals were captured more than once, the above figures total more than 32.

As determined through use of the Activity Plot, the animals were active from late morning to dusk, with most of the activity concentrated in the late afternoon. Seven captures (18.4%) occurred between 9:30 AM and 12:30 PM; 11 captures (36.9%) between 12:30 PM and 3:30 PM; 17 captures (44.7%) between 3:30 PM and 6:30 PM. No attempt was made to analyze possible seasonal changes in activity because no animals were captured during five months (December–February, July, and September) and only two were captured in October and November. Autumn through early winter (March–June) provided most of the captures.

Although Talice et al. (1960) found captive Uruguayan *M. dimidiata* to be nocturnal, under field conditions at Balcarce this was not the case. Fornes and Massoia (1965) trapped for several days in August 1963 near where Reig (1964, 1965) did most of his trapping, and captured six *M. dimidiata*. Checking their trap lines continuously during the day, and twice at night, they captured one specimen at about 1:00 PM, three at about 3:00 PM, one at 5:30 PM, and one at about 7:00 PM. The last-mentioned animal was captured near dusk or shortly after. Hunsaker and Shupe (1977) treated the Didelphidae as a whole as nocturnal. That at least one species of *Monodelphis* is diurnal, in at least part of its range, is of interest. The available data, however, concern only captures made in the spring, autumn, and winter. In the same area, the rodent *Akodon azarae* is more diurnal during winter than in summer, and this might also hold for *M. dimidiata*.

Rarely were the opossums captured more than once. Out of the 32 animals captured in the study plots, 23 were captured but once, seven twice, one thrice, and one eight times. The adult female captured three times was captured on C7 of the Hill Plot study grid on 5 November, again on 20 November, then at B5 on 18 December. The opossum captured eight times was a subadult female inhabiting the Activity Plot. She was captured on 20 March at A7, 18 April at C7 and D6, 17 May at D6 and F6, 14 June at B6 (twice), and 8 August at G6. During the approximately five-month winter period, her weight fluctuated between 12–15 g.

All *M. dimidiata* reported in this study were captured in traps baited with rolled oats. Captives were fed fresh meat, and occasionally young and adult live mice (*Mus musculus*) were offered. Female *M. dimidiata*, in particular, hesitated to kill adult mice (10–25 g in weight) and some would not attack the mice at all. After some hesitancy, most females would kill young mice. The males were more aggressive and showed little or no hesitation in killing mice, although some showed hesitancy and inexperience in killing the first one or two offered. Bertoni (1914), in writing of Paraguayan animals he identified as "Peramys brevicaudatus (*Erxl.*)" stated, "*A esta especie y congeneres las observé cazando ratas más grandes que ellas*" (This species and its congeners have been observed hunting rats larger than themselves). The reader is also referred to Bertoni, 1939, and Cabrera and Yepes, 1940, but should see Azara (1801, 1802) for somewhat different observations.

Predation upon small rodents was mentioned by Walker et al. (1975) and Hunsaker (1977) for *Monodelphis*. Although some of the Balcarce

M. dimidiata ate captive mice, particularly juvenile mice, we question whether *M. dimidiata* is an important predator of rodents. Talice et al. (1960) noted, as Dalby did in the present study, that when mice (*Mus musculus*) were introduced into an opossum cage, some opossums dispatched them right away. In other cages, however, the opossum and mouse lived together, even to sharing the same nest. Talice et al. made no mention of the sex(es) of the opossums in these encounters. If under natural conditions *M. dimidiata* is a predator on rodents, then we assume that most of the predation would be by males, and probably most of that on juveniles and nestlings.

In late summer, a moth caterpillar (family Arctiidae), feeding on the umbellifer *Eryngium paniculatum,* was common in the area. In size and appearance, these caterpillars were much like the North American woolly bear caterpillar [also an arctiid, *Isia isabella* (Smith)]. Once when one of these caterpillars was given to an opossum, it grabbed the caterpillar and rolled it with its forefeet for a minute or two. After most of the hairs were off, the opossum ate it. The manipulative handling of caterpillars during the dehairing process apparently has not been reported for other opossums. This behavior is known for other mammals (for example, skunks, *Mephitis mephitis*; Knight, 1917, and Schmidt, 1936).

Darwin (*in* Waterhouse, 1839) wrote that his specimen from Maldonado, Uruguay "Was caught by some boys digging in a garden. Its intestines were full of the remains of insects, chiefly ants and others of the Hemipterous order."

Talice et al. (1960) mentioned that, when handled, their captive animals urinated. Dalby (present study) noted that when they were agitated, such as when an intractable individual was handled, defecation could be expected. Talice et al., and Dalby as well, heard sharp, short, repeated barking sounds, particularly when an animal was disturbed. Gaping, also characteristic of other didelphids, was frequently seen. When handled often, these opossums become quite docile. A number of animals became tame to the point where they could be handled safely. Hunsaker and Shupe (1977) reported taming in response to frequent handling in *Didelphis virginiana* and *Marmosa* sp.

Litter Size, Time of Birth, and Postnatal Development

Females with young were captured only in the roadside ditches, which were irregularly trapped. The ditches, with their more mesic conditions and denser vegetation, probably contained higher numbers of *Monodelphis* than the study plot locations.

Four females gave birth in captivity. The earliest litter (16 young) of the season was found the morning of 13 December 1969, and be-

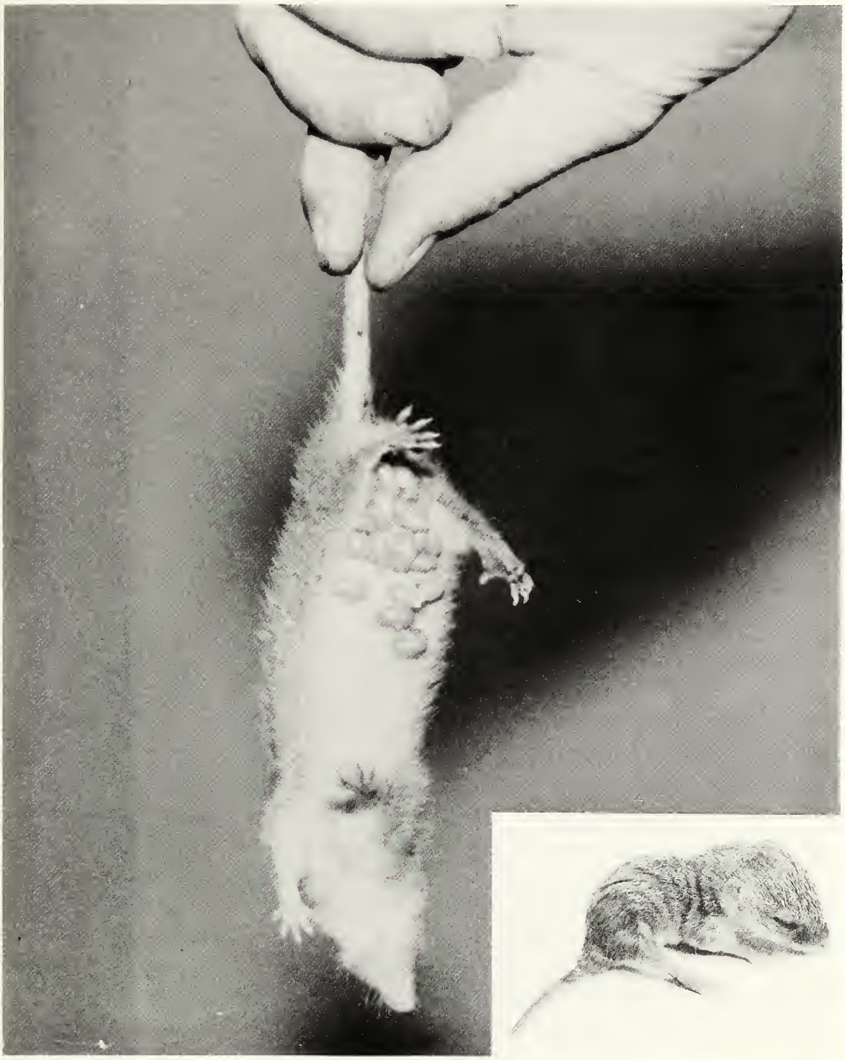

Fig. 1.—*Monodelphis dimidiata*: an adult female *M. dimidiata* with 16 newborn young attached; (inset) a young *M. dimidiata* at five weeks of age.

longed to a female (Fig. 1) that was held overnight in a trap in which she had been captured the previous afternoon. Within three days, the young had all been eaten by the mother. A female trapped several weeks earlier and caged with another female and a male was found with eight young (the entire litter?) on 4 January 1970. This female was placed in a separate cage, where she successfully raised some of the young for a period during which postnatal observations were made. A third captive female, housed with a male for an unspecified time, was found with an undetermined number of young on 15 January 1970. The male was removed and the young disappeared after several days. The fourth female, captured 13 December and housed with a male was found with an undetermined number of newborn young on 27 January. Successful mating must have occurred in captivity. The male was removed and by the next day the young were gone.

Only one previous paper (Talice et al., 1960) has reported on newborns in this species. The date of birth was not given and apparently only a single young was seen and it soon died. Judging from information presented by Walker et al. (1975) and Hunsaker (1977) on *Monodelphis,* the litter of 16 reported here is exceptionally high for the genus, with 8 to 14 young usually reported.

The postnatal development and standard measurements and weights of the one successful litter from *M. dimidiata* are as follows.

At birth (4 January).—All pink; lenses and cranial sutures visible; no pinnae or ear openings; mouth opening a small round hole at front of snout, rest of mouth represented only by a slight groove; front feet with colorless claws (deciduous?); hind feet merely large pads with a mere hint of toes, legs poorly developed, with proximal portions of ankles seemingly attached to the body; liver visible through body wall; tail always held between legs. Each of three young measured about 10 mm in crown–rump length. Weights were 0.08, 0.08, 0.11 g. Standard measurements (in mm) of the heaviest were 17-3-1-0.

One week (11 January).—No change in overall pigmentation; front feet with lightly pigmented claws; developing toes on hind feet. Able to make a soft grunt-squeak, even when attached to nipple (sound not audible beyond 30–40 cm). One young was detached from female, measured and weighed: 24-5-2-0 = 0.45 g.

Two weeks (16 January).—Some young not attached to female, being loose under female first noted several days ago; appear to be content (and alive beyond the third week). Light pigment over entire dorsum except for first millimeter of tail; thick fuzz of less than 0.5 mm in length over entire dorsum; venter fuzzy, but fuzz less dense and shorter; cranial sutures barely visible; cleft of mouth distinct; pinnae visible; claws on front feet less pigmented than previously; little development of thigh although lower leg well-developed with flexible ankle; claws beginning to form on hind feet. Young more active, able to right themselves easily. Tail not always held between legs. One young's measurements and weight: 36-5-3-1 = 0.95 g.

Three weeks (26 January).—Dorsal pigmentation darker, hair over dorsum thicker, but still less than 0.5 mm in length; venter whitish, with no distinct line of demarcation between it and dorsum; rib cage and liver visible; fur on legs and feet, almost none on tail except at base; none on ears; vibrissae present, none longer than 2 mm; hind limbs somewhat lengthened and allowing effective locomotion. When turned over, young able to right themselves immediately. Lips completely separated. One young's measurements and weight: 47-10-4-2 = 1.6 g.

Four weeks (1 February).—Hair length on dorsum 1.0–1.5 mm, 1.0 mm on venter; brownish underfur appearing on head, underfur goes from nose to a line between ears; vibrissae 3–4 mm in length; lens no longer visible through closed pigmented eyelids; hind limbs more developed although knee joint still appears inflexible during locomotion; gum line with ridges raised by development of the as yet unerupted teeth. Measurements and weights of two are: 56-12-6-3 = 2 g; 55-13-6-3 = 2 g.

Five weeks (8 February).—Underfur of dorsum well-developed, 1–1.5 mm in length, 1 mm on venter; liver and rib cage barely visible; longest vibrissae about 5 mm; knee joint movable; scrotum about 2 mm in diameter; no evidence of ability to hear; eyelids fused; anterior teeth, including incisors, nearly all erupted. Measurements of four young were: 61-14-6-4; 62-15-6-4; 62-15-6-4; 62-15-6-4 (see Fig. 1). All weighed 2 g each. Because the mother had escaped several days before, the young were killed.

The early development of the young *Monodelphis dimidiata* roughly parallels that described for *Marmosa* sp. by Eisenberg and Maliniak (1967), and for *Marmosa mitis* (=*Marmosa robinsoni*) by Barnes and Wolf (1971). Both reports stated that the young first opened their eyes at 5 to 6 weeks and were weaned at about 8 weeks. From the fused eyelids and other body features (Fig. 1), the juvenile *M. dimidiata* were nearing the time of eye opening.

From 8 February to 26 May, no data on growth of young were recorded. On the latter date, three young individuals were captured and maintained in captivity for a three-month period. Based on the reproductive data mentioned earlier, the captured young were estimated to be approximately 4 to 5 months old. Standard measurements and weights for these individuals (1 ♂, 2 ♀♀, respectively) were as follows: *Total length.*—26 May, 122, 166, 122; 1 June, 123, 117, 122; 8 June, 122, 118, 122; 14 June, 125, 122, 126; 21 June, 125, 120, 125; 28 June, 127, 124, 127; 5 July, 130, 125, 129; 12 July, 133, 125, 130; 19 July, 136, 127, 134; 26 July, 137, 126, 132; 3 August, 140, –, 132; 9 August, 147, –, 133; 16 August, 152, –, 133; 23 August, 153, –, 133;

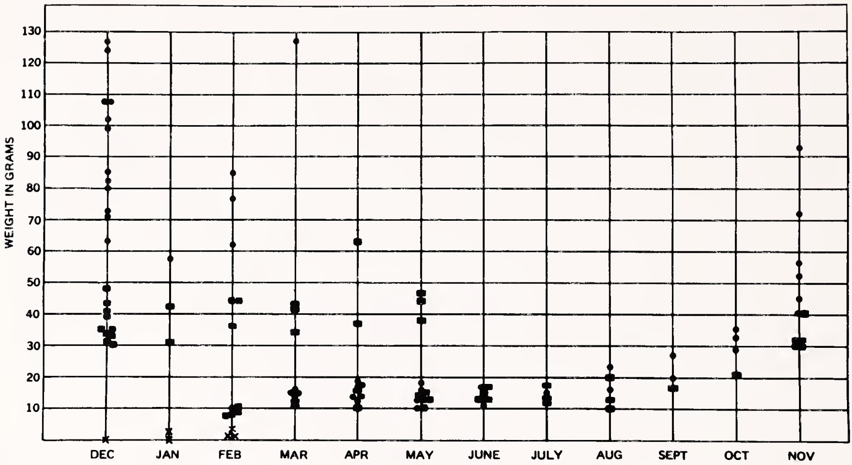

Fig. 2.—Weight distributions, shown on a monthly basis, of *M. dimidiata*. The rectangles represent females, the circles males, and the X's, very young individuals still dependent upon the females.

30 August, 155, –, 133. *Tail length.*—26 May, 37, 36, 37; 1 June, 37, 37, 37; 8 June, 36, 36, 36; 14 June, 38, 38, 38; 21 June, 38, 36, 38; 28 June, 40, 39, 39; 5 July, 41, 41, 39; 12 July, 42, 40, 38; 19 July, 42, 39, 38; 26 July, 42, 39, 37; 3 August, 42, –, 39; 9 August, 45, –, 40; 16 August, 45, –, 41; 23 August, 46, –, 41; 30 August, 48, –, 41. *Hind foot.*—26 May, 12, 11, 11; 1 June, 12, 11, 11; 8 June, 12, 11, 12; 14 June, 12, 11, 12; 21 June, 12, 11, 11; 28 June, 12, 11, 12; 5 July, 12, 11, 11; 12 July, 12, 11, 12; 19 July, 12, 11, 12; 26 July, 12, 12, 12; 3 August, 12, –, 12; 9 August, 13, –, 12; 16 August, 13, –, 12; 23 August, 13, –, 12; 30 August, 13, –, 12. *Ear.*—no growth noted—measurements fluctuated stochastically from 9 (one reading) to 10 (32 values) and 11 (7 readings). *Weight.*—26 May, 14, 12, 14; 1 June, 14, 10, 16; 8 June, 14, 10, 14; 14 June, 17, 13, 17; 21 June, 16, 13, 18; 28 June, 15, 11, 17; 5 July, 16, 12, 17; 12 July, 16, 12, 17; 19 July, 16, 13, 17; 26 July, 16, 8, 16; 3 August, 18, –, 16; 9 August, 24, –, 20; 16 August, 24, –, 20; 23 August, 27, –, 20; 30 August, 29, –, 19. The first-listed female was loose on 25 July, recaptured, showing a significant weight loss, on 26 July, and escaped permanently before 3 August. The two remaining animals were killed accidentally after 30 August.

The beginning of molt was noted in one subadult (20 g) male captured in late winter–early spring (mid-September 1969). The progress of the molt was followed in the lab. Molt was first evident only on a small dorsal area of the neck and adjacent back. By mid-October, the molt line had moved laterally to encompass the shoulder blades and sides, and dorsally and posteriorly nearly to the hindquarters. Anteriorly, the molt line extended to the level of the eyes. By mid-November, molt was essentially completed, and the male weighed about 55 g. The new coat color was more dusky than the previous coat, lacking the reddish cast of the former.

A monthly weight profile is presented in Fig. 2. The data were taken from freshly trapped animals and also from those maintained in captivity for various lengths of time. The months of birth documented for the Balcarce area are December and January, and perhaps the first part of February (the last recorded birth occurred in the last week of January). Young animals, weighing 8–10 g, were first captured in February. Growth in the unheated lab and in the field was very slow until early spring, when weights started to increase rapidly. The young developed rather slowly through the cooler months, as documented by the laboratory, field, and morphometic data. Spring growth, especially in the males, and sexual maturation were rapid, quickly preparing these opossums for that summer's reproductive period.

All reproduction in this population appears to be dependent upon the attainment of sexual maturity by young animals, hence the late (December–January) breeding period. At the latitude of Balcarce, these young animals simply cannot reach sexual maturity before December. The evidence presented in this paper, and earlier by Reig (1964, 1965), indicates that older animals rarely, if at all, survive to the following breeding season. Thus, at least at this latitude, breeding is performed only by young of the preceding year.

The sexes grew at comparable rates until early spring, at which time the growth rate of both sexes increased markedly with the males outstripping the females. A stub-tailed male captured on 20 September 1969 and weighing 20 g weighed 56 g by 17 November—a weight that placed it within the lower limits of those given for that time period in Figure 2. During one week (27 October–3 November) when an abundance of fresh meat was available, this animal went from 34 g to 43 g, a gain of 9 g, while during the next week, it lost several grams (3 November, 40 g). By the following week (10 November), the male weighed 56 g, a gain of over 2 g per day. From October to November, males went from a 32 g (n = 3) to a 60 g average (n = 6), nearly doubling their weight. Females in this same period went from approximately 21 g (n = 1) to an average of 33 g (n = 5)—about a 60% increase. Weights and measurements of mature males and females for the months of December–March were: *total length*, ♂♂, 230, 215, 216, 213, 211, 207; ♀♀, 175, 180, 188, 191, 180; *tail length*, ♂♂, 76, 50, 71, 48, 58, 63; ♀♀, 57, 56, 60, 59, 55; *hind foot* (c.u.), ♂♂, 10(?), 18, 18, 19, 18, 18; ♀♀, 13, 15, 15, 16, 15; *ear* (from notch), ♂♂, 11, 12, 12, 12, 13, 11; ♀♀, 8, 11, 11, 11, 10; *weight,* ♂♂, 99, 102, 57, 85, 77, 62; ♀♀, 31, 44, 43, 42, 34. Females weighed only 40% as much as males, but reached 85% of the males' total length. The measurements of these animals agree with those of the members of the age classes 6 and 7 (Fig. 3). According to Ralls (1976), when females are considerably smaller than males, they typically cease growth at an earlier age than males and also begin sexual activity sooner. In *M. dimidiata,* however, contemporaneous differential growth rates appear especially important. Reig's (1964, 1965) and our conclusions in regard to *M. dimidiata* are in contrast to those of Woolley (1966), Wood (1970), and others for certain dasyurid marsupials, which are somewhat similar in appearance to *Monodelphis dimidiata.* In the Australian animals, all of the males die at the end of their first (and thus only) period of sexual activity although the females are capable of surviving at least two breeding seasons.

Although an annual pattern appears clear enough in the Balcarce area, somewhat different patterns, as yet not understood, exist to the north (data largely supplied by Charles O. Handley, Jr.). The juvenile holotype of *Monodelphis fosteri* Thomas from Caleufú, Argentina (35°35′S, 64°30′W), taken on 10 April, and a series of seven juveniles taken by Oldfield Thomas at Colón, Uruguay (34°48′S, 56°14′W), would match the situation found in Balcarce, but the adult male (Thomas, 1888) holotype of *Monodelphis dimidiata* taken in June (Waterhouse, 1839) at Maldonado, Uruguay (34°54′S, 54°57′W), and the single adult females taken at Pergamino, Argentina (33°55′S, 60°32′W), on 14 August and at Río Ceballos, Argentina (31°07′S, 64°18′W), on 28 September would not.

Walker et al. (1975) and Hunsaker (1977) wrote that tropical species of *Monodelphis* apparently breed throughout the year. Certainly this appears to be the case with *M. domestica* in Brazil (Streilein, 1982*a,* 1982*b*), although *M. brevicaudata* may be seasonally polyestrous in Venezuela (O'Connell, 1979). At Balcarce, at least, year-round reproductive activity in *M. dimidiata* does not occur. We also have no evidence to suggest more than one bout of reproductive activity per female during the year. Hunsaker (1977) has written that tropical species of *Marmosa* breed throughout the year, but those in cool and temperate zones breed once. The same pattern may apply to *Monodelphis.* The lateness of breeding in *Monodelphis dimidiata* (this study), comparable to June and July in equivalent northern latitudes, is rather unusual. Because *Monodelphis dimidiata* is pouchless, perhaps a relatively late breeding season is more advantageous than an earlier one in a temperate environment, considering the altricial state of the young.

Although there is a life expectancy in *Marmosa robinsoni* of about three years in captivity, Hunsaker (1977) stated that reproductive abil-

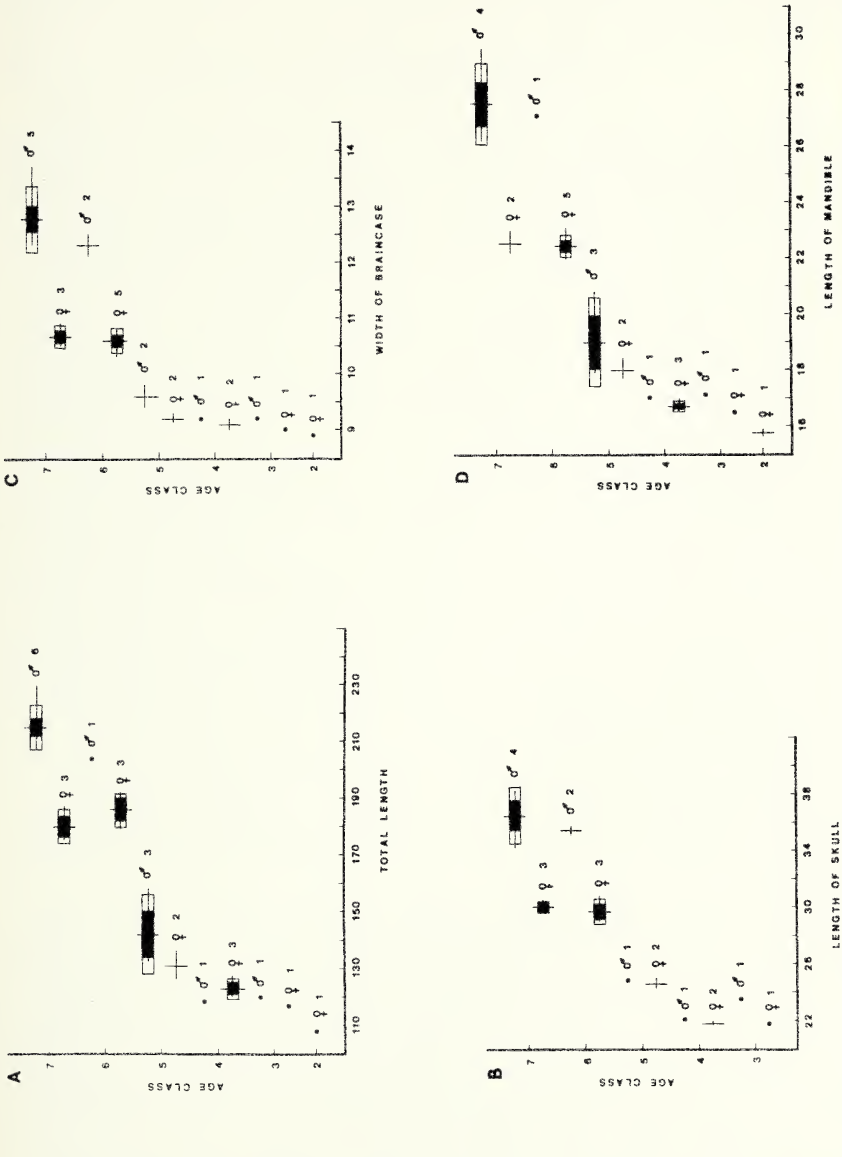

Fig. 3.—Graphs of measurements of *M. dimidiata* of both sexes and different age classes. A) total length; B) length of skull; C) width of braincase; D) length of mandible (ramus).

ity fades during the second year, and life expectancy is probably less than a year in nature. Thus, species of both *Marmosa* and *Monodelphis* apparently use a strategy of high production to compensate for high mortality and a rapid population turnover.

LIFE HISTORY STRATEGY IN *MONODELPHIS DIMIDIATA*: APPARENT SEMELPARITY

Cole (1954) defined "semelparity" as "multiplying once in a lifetime." He did not discuss situations in which males took part in but one breeding season but females (or at least some of them) were iteroparous (having more than one clutch, litter, etc., in a lifetime). Lee et al. (1977) and Braithwaite and Lee (1979) have used the word "semelparity" to describe the latter phenomenon. This practice seems unacceptable. "Semelparous" means "giving birth but once." As males never give birth at all, to apply the adjective to them seems ridiculous. To say a species exemplifies semelparity when, in fact, the females are iteroparous also seems absurd. Cole's concern was primarily litters, not times of rut. Also, semelparity, as Cole used the term, has certain consequences on population growth rates—consequences not realized if, in fact, the females are iteroparous. We propose to call species in which males have but a single period of "rut" *semelseminant.* Those in which there are two or more periods of "rut" we call *iteroseminant.* As far as we know, all species that are semelparous (*sensu stricto*) are also semelseminant. Until an exception is brought to our attention, we will assume all organisms to which the term semelparous is properly applied are ones in which there is but one "litter" and one period of "rut." Therefore, if we use the term semelseminant to descibe a species, we imply that the female is iteroparous. The word semelseminant, as defined here, implies nothing about the duration of the single period of reproductive capability nor the number of females impregnated or times a single polyestrous female may be so in a reproductive season. Thus, even humans and certain domestic animals can be regarded as semelseminant.

The weight distributions shown in Fig. 2 suggest that the adult *Monodelphis dimidiata* do not survive the winter (or into the winter), thus indicating semelparity. In addition, as Reig (1964) wrote (translated from Spanish), "only in the month of January were adults obtained. All . . . captured in . . . April, June, August, and September were young . . . It is possible we have here an animal with a growth curve . . . that suddenly increases with the advance of spring and the advent of sexual maturity—the adult individuals of large size dying at the beginning of the first autumn frost." See also Reig (1965).

Monodelphis dimidiata was the first (and remains the only) warm-blooded vertebrate for which true semelparity as defined here has been hypothesized, notwithstanding the statement of Lee et al. (1977) that, "It has not previously been described in mammals or birds" (see also Braithwaite and Lee, 1979). These latter authors were reporting supposed semelparity (actually semelseminance) in the dasyurid marsupial genus *Antechinus.* In fact, annual, semelseminant males were reported for *Microtus* as early as 1933 by Baker and Ranson.

It is of interest that in the semelseminant species *Antechinus stuartii,* at least, "Male[s] . . . are considerably larger than females throughout life" (Wood, 1970). According to Williams (1966*a*), extreme sexual dimorphism may be expected to be correlated with semelparity (or presumably in the case of the *Antechinus,* with the semelseminant condition) as would aggressive behavior between males.

Monodelphis dimidiata may also be one of the few warm-blooded vertebrates in which both sexes are thought to be "annuals." Semelparous animals are not, of course, necessarily "annuals" (see Cole, 1954). Williams (1957) gave an explanation of virtually immediate postbreeding mortality in semelparous species. See Baker and Ranson (1933), Hamilton (1937), and Elton (1942) concerning voles which are annuals or essentially so.

According to Braithwaite and Lee (1979), "The largest known litter sizes in small dasyurids occur in species with semelparous males (10–12 neonates), although certain species with this strategy have litter sizes similar to those with iteroparous males (eight or less, occasionally nine or 10 neonates . . .)." Assuming that some species of *Monodelphis* may be semelparous and others iteroparous, and that semelparous species may produce the largest number of neonates, and that number of neonates may be correlated with number of nipples, one might be able to predict which *Monodelphis* (and other didelphids?) are semelparous on the basis of number of nipples in the females (male marsupials have no trace of nipples). *Monodelphis dimidiata* appears to be semelparous and has enough nipples to suckle at least 16 young (Fig. 1). *Monodelphis henseli* (=*M. sorex*?) with 17 to 27 nipples (Thomas, 1888), may prove to be semelparous, whereas at least one member of the *Monodelphis brevicaudata* group, with a smaller number of nipples (Pine, 1980), apparently is not (O'Connell, 1979). Streilein (1982*b*) reported an *M. domestica* that produced two litters. According to Thomas (1923), *M. domestica* has 11 or 13 nipples. Even if the issue of semelparity versus iteroparity were not involved, however, we might expect *M. dimidiata* and *M. henseli* to have relatively high numbers of mammae. As noted by Lord (1960), there is a positive correlation between litter size and latitude, and the two species in question are among the southernmost *Monodelphis* (see also Cody, 1966; Pianka, 1970). MacArthur and Wilson (1967) wrote, "where climates are rigorously seasonal and winter survivors recolonize each spring, in the presence of a bloom of foliage and food, we expect *r* selection favoring large productivity." Both *M. dimidiata* and *M. henseli,* however, show extreme sexual dimorphism as compared to most other *Monodelphis,* and this characteristic has been noted in non-mammalian vertebrate semelparous annuals (Myers, 1952; Storey, 1940).

M. dimidiata would seem to be producing far more neonates than can later be weaned. This appears to be the usual case in didelphids, but *M. dimidiata* is an extreme instance. According to Low (1978), "When the time of risk for offspring falls early within the period of parental effort and is predictable, even if unavoidable by increased PI [=parental investment, the portion of parental effort (PE) received by each offspring such that $\sum$ PI = PE for any period under consideration], parents may be able to profit by starting more offspring than they could otherwise raise, investing minimally until the high-risk period is past and then investing maximally." Perhaps this situation occurs in *Monodelphis dimidiata,* although potential risks suffered by attached neonates are unknown. Low also noted, "In some cases the PE invested in offspring which later die may be partly recovered . . . when the parent or surviving offspring eat the . . . carcasses of dead juveniles." The cannibalizing reported here of young *M. dimidiata* by their mothers is of interest in this regard. Might free-living *M. dimidiata* females cannibalize some of their young (even if alive) during times of stress? During a "good year" more young might be safe from being eaten than during a "bad year." The female could adapt her maternal behavior to changing conditions. Eating *all* her young has no selective advantage in a semelparous animal unless termination of lactation could allow a female to escape the physiological exhaustion following weaning and thus perhaps survive into a new breeding season.

NON-GEOGRAPHIC VARIATION

Variation with Age

As the sample sizes representing most age classes were small, we did not test for differences. Fig. 3 shows the general trends of increasing dimensions in four selected characters for both sexes in going from younger to older age classes. Detailed data are presented in Table 1. In general, there were no apparent differences between males and females in the same age class until age class 5, at which stage males began to be larger than females. Gardner (1973) found a similar situation in *Didelphis,* in which genus the differences between males and females began at his age class 4. In *Monodelphis dimidiata* from Balcarce, males are substantially larger by age class 6 for all measurements except tail length, M1–M4 length, and width of postorbital constriction.

The development of the lambdoidal and sagittal crests also follows a characteristic general growth pattern. Each age-sex class was scored, as to development of a crest, as follows: 1) no indication of a crest; 2) a slight ridge present; 3) a definite ridge present; and 4) a highly developed ridge present. In the specimens of *M. dimidiata* from Balcarce, a female of age class 2 showed no indication of either crest. All individuals (both male and female) of age classes 3 through 5 were scored as 2 and 1, respectively, as to lambdoidal and sagittal crests. All females of age classes 6 and 7 showed a definite lambdoidal crest and a slight sagittal crest—whereas most males of age classes 6 and 7 had both crests well-developed. One male of age class 7 had both crests highly developed. These comparisons were based upon proportional development of the crests and not on absolute size. As adult males are larger than females, the absolute size of the crests would be expected to be greater in males, but the sexual difference goes beyond that and would appear to be allometric in nature.

The most marked development of cranial crests occurs between age classes 5 and 6. Because little change was evident in this and other characters between age classes 6 and 7, members of both age classes are treated here as adults. We also noted that for each sex there was no overlap in size between individuals of age classes 5 and 6 for most characters.

Individual and Secondary Sexual Variation

One male showed fusion of the first and second left lower premolars (see Fig. 4). Torre and Dysart (1966) reported fused incisors in *Didelphis* and summarized the literature on fused teeth in mammals.

Basic statistics for adults are presented in Table 2. Individual variation is most clearly expressed by the coefficients of variation (CV). Among external characters, males had higher CV's than females for total length and tail length, whereas females were more variable in length of hind foot and ear. The extremely high CV's for tail and ear lengths may be artifacts of either measuring techniques or small sample size. However, in most mammals, external characters have been shown to be generally more variable than cranial characters (Long, 1968, 1969; Yablokov, 1974). Males were more variable in 12 of the 13 cranial characters studied. Females were more variable only in M1–M4, and these CV's were of the same magnitude. The CV's for cranial characters averaged more than half again as large in males as in females (the mean CV for males was 4.65, and for females, 2.87). Long (1969) considered cranial measurement CV's between 2.5 and 5.3 to be normal for mammals in general. Male *M. dimidiata* had CV's higher than 5 in nasal length, postorbital constriction, and mandibular depth. Only mandibular depth had a CV sufficiently high (8.45) as to bring into question

Table 1.—*Summary statistics on age variation in* Monodelphis dimidiata *from Balcarce area, Argentina. Under each age and sex class, for each measurement, the first line is the mean with sample size in parentheses; the second line is the range; the third line is the standard deviation with the coefficient of variation in parentheses.*

		Age class					
Measurement	Sex	2	3	4	5	6	7
Total length	Females	108 (1) —	117 (1) —	123.00 (3) 120–127 3.61 (2.93)	131.00 (2) 126–136 —	186.00 (3) 179–191 6.24 (3.36)	180.67 (3) 175–187 6.03 (3.34)
	Males	—	120 (1) —	119 (1) —	142.00 (3) 132–158 14.00 (9.86)	204 (1) —	215.33 (6) 207–230 7.86 (3.65)
Tail length	Females	30 (1) —	38 (1) —	35.67 (3) 35–37 1.15 (3.24)	41.00 (2) 38–44 —	58.67 (3) 57–60 1.53 (2.60)	55.33 (3) 54–57 1.53 (2.76)
	Males	—	40 (1) —	34 (1) —	41.67 (3) 37–48 5.69 (13.65)	58 (1) —	61.00 (6) 48–76 11.21 (18.38)
Hind foot (c.u.)	Females	11 (1) —	12 (1) —	11.67 (3) 11–12 0.56 (4.95)	12.00 (2) 12–12 —	15.33 (3) 15–16 0.58 (3.76)	14.33 (3) 13–15 1.15 (8.02)
	Males	—	12 (1) —	12 (1) —	14.00 (2) 13–15 —	19 (1) —	18.33 (6) 18–19 0.52 (2.84)
Ear (from notch)	Females	8 (1) —	10 (1) —	9.00 (3) 9–9 0.00 (0.00)	9.50 (2) 9–10 —	10.67 (3) 10–11 0.58 (5.41)	9.00 (2) 8–10 —
	Males	—	10 (1) —	10 (1) —	10.00 (3) 10–10 0.00 (0.00)	13 (1) —	11.83 (6) 11–13 0.75 (6.34)
Skull length	Females	—	22.8 (1) —	22.85 (2) 22.8–22.9 —	24.65 (2) 24.4–24.9 —	29.70 (3) 29.0–30.7 0.89 (2.99)	30.07 (3) 29.8–30.5 0.38 (1.26)

Table 1.—*Continued.*

Measurement	Sex	Age class 2	3	4	5	6	7
	Males	—	23.5 (1) —	23.1 (1) —	24.9 (1) —	35.55 (2) 35.5–35.6 —	36.48 (4) 34.2–38.2 1.95 (5.35)
Condyloincisive length	Females	—	22.4 (1) —	22.40 (2) 22.3–22.5 —	24.20 (2) 23.8–24.6 —	29.30 (4) 28.5–30.2 0.70 (2.38)	29.45 (2) 29.3–29.6 —
	Males	—	23.1 (1) —	22.9 (1) —	25.95 (2) 24.4–27.5 —	35.20 (2) 35.2–35.2 —	36.33 (3) 33.7–37.9 2.29 (6.31)
Palatal length	Females	11.5 (1) —	11.9 (1) —	12.17 (3) 12.1–12.2 0.06 (4.74)	13.15 (2) 13.0–13.3 —	15.18 (5) 14.9–15.7 0.31 (2.05)	15.85 (2) 15.3–16.4 —
	Males	—	12.3 (1) —	12.1 (1) —	13.70 (3) 13.0–15.0 1.13 (8.22)	17.80 (4) 17.3–18.1 0.36 (2.00)	18.04 (5) 17.1–19.2 0.96 (5.32)
Greatest nasal length	Females	9.1 (1) —	9.3 (1) —	9.53 (3) 9.3–9.9 0.32 (3.37)	11.10 (2) 10.9–11.3 —	12.22 (4) 11.8–12.6 0.35 (2.86)	12.43 (3) 12.2–12.6 0.21 (1.67)
	Males	—	9.7 (1) —	9.9 (1) —	10.70 (2) 10.6–10.8 —	14.95 (4) 14.5–15.4 0.37 (2.47)	15.13 (7) 14.0–16.4 0.97 (6.42)
Zygomatic breadth	Females	10.7 (1) —	11.2 (1) —	11.60 (2) 11.5–11.7 —	11.9 (1) —	15.75 (4) 15.5–16.0 0.21 (1.32)	16.15 (2) 16.0–16.3 —
	Males	—	11.9 (1) —	11.4 (1) —	12.3 (1) —	20.35 (2) 20.2–20.5 —	21.03 (3) 19.8–22.3 1.25 (5.94)

Table 1.—*Continued.*

Measurement	Sex	Age class					
		2	3	4	5	6	7
Postzygomatic braincase width	Females	8.9 (1) —	9.0 (1) —	9.10 (2) 9.0–9.2 —	9.20 (2) 9.1–9.3 —	10.58 (5) 10.3–10.8 0.22 (2.05)	10.67 (3) 10.5–10.9 0.21 (1.97)
	Males	—	9.2 (1) —	9.2 (1) —	9.60 (2) 9.4–9.8 —	12.30 (2) 12.1–12.5 —	12.78 (5) 12.3–13.7 0.58 (4.54)
M3–M3	Females	—	7.3 (1) —	7.37 (3) 7.2–7.5 0.15 (2.07)	7.60 (2) 7.5–7.7 —	8.86 (5) 8.8–8.9 0.05 (0.62)	9.05 (2) 9.0–9.1 —
	Males	—	7.3 (1) —	7.1 (1) —	7.77 (3) 7.4–8.0 0.32 (4.14)	9.75 (4) 9.5–10.0 0.24 (2.44)	10.03 (7) 9.6–10.8 0.47 (4.70)
Maxillary toothrow	Females	—	—	9.45 (2) 9.4–9.5 —	9.95 (2) 9.9–10.0 —	11.04 (5) 10.9–11.2 0.11 (1.03)	10.95 (2) 10.8–11.1 —
	Males	—	—	—	10.50 (2) 10.0–11.0 —	12.10 (2) 12.0–12.2 —	12.48 (5) 11.8–13.0 0.46 (3.68)
M1–M4	Females	—	—	5.30 (2) 5.3–5.3 —	5.65 (2) 5.6–5.7 —	5.46 (5) 5.4–5.5 0.05 (1.00)	5.33 (3) 5.1–5.6 0.25 (4.69)
	Males	—	—	—	5.50 (3) 5.4–5.6 0.10 (1.82)	5.52 (4) 5.3–5.7 0.17 (3.09)	5.50 (7) 5.2–5.6 0.14 (2.54)
Postorbital constriction	Females	4.85 (2) 4.8–4.9 —	5.1 (1) —	5.05 (2) 4.9–5.2 —	5.15 (2) 5.1–5.2 —	5.10 (5) 5.0–5.4 0.17 (3.40)	5.13 (3) 5.1–5.2 0.06 (1.13)

Table 1.—*Continued.*

Measurement	Sex	Age class					
		2	3	4	5	6	7
	Males	—	5.1 (1) —	5.2 (1) —	5.10 (3) 4.9–5.3 0.20 (3.92)	5.00 (4) 4.5–5.3 0.42 (8.48)	4.96 (7) 4.6–5.2 0.21 (4.23)
Mandibular depth	Females	—	—	1.8 (1) —	1.95 (2) 1.8–2.1 —	2.68 (5) 2.6–2.8 0.08 (3.12)	2.67 (3) 2.6–2.7 0.06 (2.10)
	Males	—	—	—	2.20 (3) 2.0–2.4 0.20 (9.09)	3.47 (3) 3.4–3.6 0.12 (3.33)	3.67 (7) 3.3–4.2 0.36 (9.81)
Length of ramus	Females	15.75 (2) 15.6–15.9 —	16.5 (1) —	16.73 (3) 16.5–16.9 0.21 (1.24)	18.05 (2) 17.7–18.4 —	22.46 (5) 22.0–23.1 0.42 (1.88)	22.55 (2) 22.2–22.9 —
	Males	—	17.1 (1) —	17.0 (1) —	18.97 (3) 17.9–20.8 1.59 (8.41)	27.1 (1) —	27.55 (4) 26.2–29.5 1.39 (5.04)
Mandibular toothrow	Females	—	11.8 (1) —	11.73 (3) 11.5–11.9 0.21 (1.77)	12.20 (2) 12.2–12.2 —	13.38 (5) 13.1–13.5 0.16 (1.23)	13.10 (2) 12.9–13.3 —
	Males	—	12.0 (1) —	11.8 (1) —	12.57 (3) 11.8–13.4 0.80 (6.38)	14.7 (1) —	14.90 (4) 14.3–15.8 0.70 (4.70)

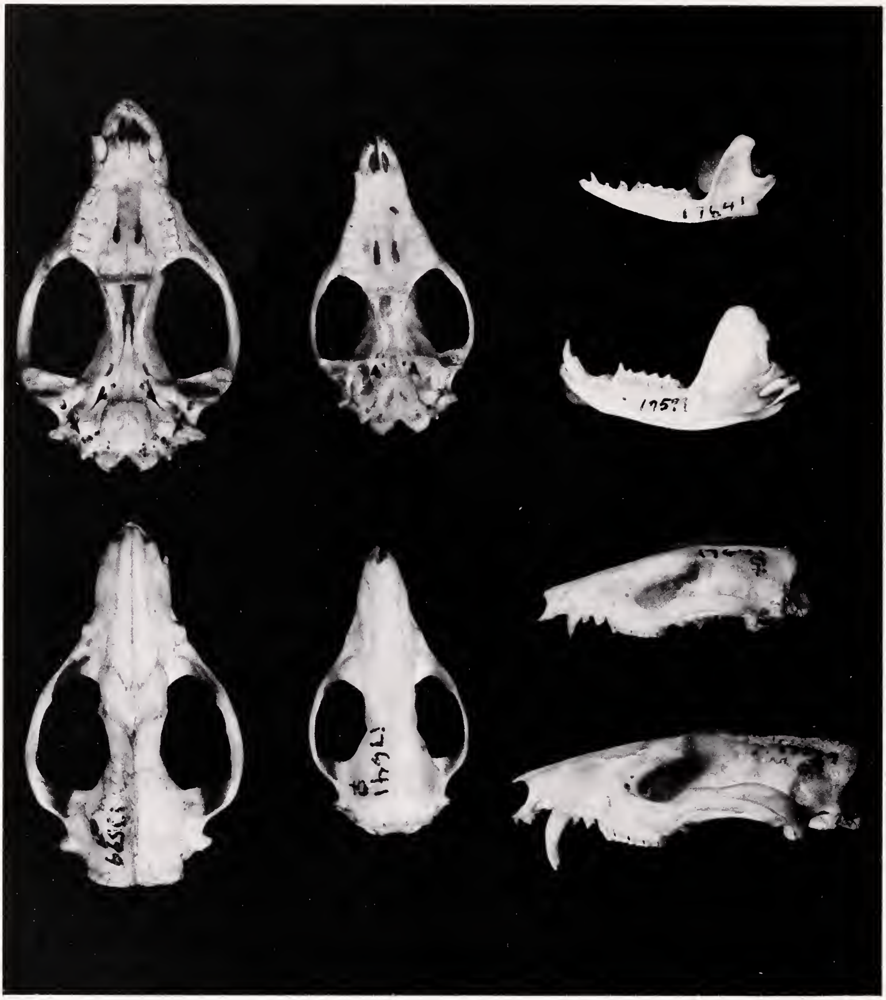

Fig. 4.—Skulls of adult (age class 7) male and female *M. dimidiata*.The male is to the left or is the lower in each pair. Note larger, more robust skull with stronger crests in male—also longer canines. In left mandibular ramus of male, the first two premolars are fused (an abnormality). Note cutting edge of third lower premolar, which forms a carnassial-like pair of shearing teeth with upper third premolar. Photograph is 1.2×.

its utility in systematic studies. Females had no CV's over 5 and most were below 2.0. A possible explanation for the differences between male and female variability may be related to the reproductive energetics hypothesis of Gardner (1973) for the genus *Didelphis.* Adult females thus show less variability owing to a virtual cessation of growth after attainment of a certain size, whereas males are more variable because they continue growing throughout life.

The results of analyses of variance between adult males and females for each character are given in Table 2. Of the 17 characters, 14 were significantly different, with males being larger in each case. In the three characters that were not significantly different, males averaged slightly larger in tail length and in M1–M4, whereas females were slightly larger in postorbital constriction. Overlap in measurements occurred in tail length, ear length, M1–M4, and postorbital constriction.

The extreme sexual dimorphism (Fig. 4) in absolute size and in relative variability necessitates treating the sexes separately in systematic work. Although similar to the situation described by Gardner (1973), the magnitude of sexual dimorphism in *M. dimidiata* is much greater, and the variability within the population studied considerably less, than that in populations of *Didelphis.* Ralls (1977) listed the Marsupialia as one of the orders that contain "extreme cases of sexual dimorphism favoring males, defined as a ratio of average male to female weights greater than 1.6." The condition in marsupials was known to Ralls only in the Macropodidae. On the basis of our studies of *M. dimidiata,* the Didelphidae will have to be added to the "extreme sexual dimorphism favoring males" category. Ralls' statement, "In the Marsupialia and the Chiroptera the extremely dimorphic species are found in the families which have the largest modal species size in their orders" will also now need to be modified.

One specimen (MSU 17887) was excluded from the study of nongeographic variation. Placed in age class 6, it was labelled as a male but the development of the cranial crests matched that in females of the same age class. Perhaps the sex was incorrectly recorded for this specimen. On the other hand, Gardner (1973) found occasional reversal of the usually sexually dimorphic skull characters in *Didelphis,* and MSU 17887 may be an example of the same sort of phenomenon in *Monodelphis dimidiata.*

The usual size and proportional differences between the skulls of adult *Monodelphis dimidiata* of different sexes are quite extreme. The differences are sufficiently great that a taxonomist examining a small sample might easily be led to treat females and young males as one species, and adult males as another. The molars are of about the same size, however, and this factor is useful when making comparisons of what are apparently similar species of opossums that differ in size.

Compared to those of the females, the skulls of males are not only much larger, but more massive with proportionately larger crests. They have enlarged postorbital processes of the frontals, or at least heavy ridges in that area, more flaring zygomatic arches, sabre-like canines,

Table 2.—*Basic statistics for and results of analyses of variance between male and female* Monodelphis dimidiata *(age classes 6 and 7 combined) from Balcarce area, Argentina. In each column are presented the mean ± 1 standard deviation followed by the range and the coefficient of variation for each measurement. F-values with *, **, and *** represent significance levels of* $P \leq 0.05, 0.01,$ *and* 0.001*, respectively.*

Measurement	Males		Females		F-value
	N	$\bar{X}$ ± 1 SD	N	$\bar{X}$ ± 1 SD	
Total length	7	213.71 ± 8.36 204–230 3.91	6	183.33 ± 6.22 175–191 3.39	53.53***
Tail length	7	60.57 ± 10.29 48–76 16.99	6	57.00 ± 2.28 54–60 4.00	0.68 ns
Hind foot (c.u.)	7	18.43 ± 0.53 18–19 2.90	6	14.83 ± 0.98 13–16 6.63	70.34***
Ear (from notch)	7	12.00 ± 0.82 11–13 6.80	5	10.00 ± 1.22 8–11 12.00	11.67**
Skull length	6	36.17 ± 1.58 34.2–38.2 4.38	6	29.88 ± 0.64 29.0–30.7 2.15	81.06***
Condyloincisive length	5	35.88 ± 1.74 33.7–37.9 4.84	6	29.35 ± 0.55 28.5–30.2 1.89	76.94***
Palatal length	9	17.93 ± 0.72 17.1–19.2 4.04	7	15.37 ± 0.52 14.9–15.7 3.40	61.93***
Greatest nasal length	11	15.06 ± 0.78 14.0–16.4 5.21	7	12.31 ± 0.30 11.8–12.6 2.41	77.34***
Zygomatic breadth	5	20.70 ± 0.99 19.8–22.3 4.81	6	15.88 ± 0.28 15.5–16.3 1.75	131.14***
Postzygomatic braincase width	7	12.64 ± 0.54 12.1–13.7 4.28	8	10.61 ± 0.20 10.3–10.9 1.91	97.74***
M3–M3	11	9.93 ± 0.41 9.5–10.8 4.16	7	8.91 ± 0.11 8.8–9.1 1.20	40.22***
Maxillary toothrow	7	12.37 ± 0.43 11.8–13.0 3.45	7	11.01 ± 0.13 10.8–11.2 1.22	64.57***
M1–M4	11	5.51 ± 0.14 5.2–5.7 2.62	8	5.41 ± 0.16 5.1–5.6 2.87	2.08 ns

Table 2.—*Continued.*

	Males		Females		
Measurement	N	$\bar{X}$ ± 1 SD	N	$\bar{X}$ ± 1 SD	F-value
Postorbital constriction	11	4.97 ± 0.28 4.5–5.4 5.69	8	5.11 ± 0.14 5.0–5.4 2.65	1.66 ns
Mandibular depth	9	3.60 ± 0.30 3.3–4.2 8.45	8	2.68 ± 0.07 2.6–2.8 2.64	69.38***
Length of ramus	5	27.46 ± 1.22 26.2–29.5 4.45	7	22.49 ± 0.40 22.0–23.1 1.79	103.80***
Mandibular toothrow	5	14.86 ± 0.61 14.3–15.8 4.12	7	13.30 ± 0.22 12.9–13.5 1.68	39.61***

the anterior end of the lower jaw bent upwards, proportionately deeper lower jaws, a strongly-developed postorbital constriction, and a larger notch in the maxilla to receive the lower canine. A number of these male characteristics were used in Cabrera's (1919) diagnosis of *Minuania* (regarded by him as a genus in 1919, a subgenus in 1958) from which we can assume that Cabrera was unfamiliar with the characteristics of adult females.

Although fairly extreme sexual differences in size have been found in both North American *Didelphis* (Gardner, 1973), *Marmosa* (Tate, 1933), and in *Monodelphis,* it does not exist in all species of didelphids—not being found, for example, in *Marmosa parvidens* Tate (Pine, 1981). Gardner (1973) cited Lowrance (1949) in noting that bone growth continues throughout the life of the individual in at least some species of opossums. According to Gardner, "size differences between sexes become accentuated following the attainment of reproductive maturity . . . suggesting that the nutritional load placed on pregnant and lactating females diverts energy sources that would otherwise contribute to increased growth." Assuming these considerations apply to some extent to *M. dimidiata,* then gestation, and not lactation, would have to be the more responsible for the sexual dimorphism in size. By the time the young are born, the adult males have already achieved large size. The gestation period is unknown in *M. dimidiata* but is fairly long (26–35 days) in *Antechinus stuartii* (Woolley, 1966 *fide* Lee et al., 1977). Examination of Fig. 2 seems to indicate that in *M. dimidiata,* the males may begin to outstrip the females in size before sexual maturity is attained, unless sexual maturity is reached considerably before growth stops and the gestation period is exceedingly long (parturition occurred in captives from the middle of December until late January).

According to Williams (1966*b*), strong sexual dimorphism is indicative of high reproductive effort. In those didelphids that show it, this correlation may be owing to very direct causation—the actual investment being responsible for the dimorphism rather than its being brought about by such common means as the difference in the sex chromosome complement.

Whatever its cause, the extreme dimorphism in *Monodelphis dimidiata* may result in a certain amount of ecological role separation—a result that might be beneficial to survival of individuals and the species. Such role separation may be hinted at by the differential tendency we noted in the two sexes to attack and eat mice. Downhower's (1976) observation that "Agonistic encounters are likely to reduce the time available for foraging and thus larger size may provide males with the physiological reserves necessary to hold a territory" may have relevance for *M. dimidiata.* As presumed semelseminant annuals, the males may find it to their "advantage" virtually to abandon foraging during the mating season. Downhower's observation that when food is abundant, smaller individuals can replenish their stored energy reserves faster than larger individuals can may also have relevance for female *M. dimidiata.* Selander (1958) found a positive relationship between polygamous or promiscuous mating relationships and degree of size difference by sex in icterids. Orians (1969) discussed this sort of relationship in other animals, including mammals. Male *Monodelphis dimidiata* presumably are promiscuous.

ABBREVIATED HISTORY RELATING TO THE NAME *MONODELPHIS DIMIDIATA*

1838. Waterhouse first mentioned the animal now known as *Monodelphis dimidiata* (Wagner) under the name "Didelphis brachyura. Gmel." This and later references by Waterhouse (1839, 1841, 1843, 1846) were based on a specimen brought back by Darwin from Maldonado, Uruguay.

1847. Wagner named Darwin's animal *D*[*idelphys*]. *dimidiata.*

1854. Burmeister called Darwin's animal *Didelphys brachyura.*

1855. Schreber included it in "*D*[*idelphys*]. *brachyura* SCHREB."

1856. Burmeister referred Darwin's animal to *Microdelphys brachyura.*

1873. Hensel used the name *Microdelphys brachyura* for a Brazilian animal.

1882, 1887. Arechavaleta (*fide* Ximénez et al., 1972) discussed the Uruguayan distribution of *Monodelphis dimidiata* under the name *Didelphis brachyura.*

1888. Beddard described the sternal gland of *Didelphys dimidiata.* Thomas used this same name for specimens from Taquara and San Lorenzo (=São Lourenço do Sul), Rio Grande do Sul, Brazil. All of the specimens available to Thomas were males as his redescription clearly indicates (see discussion on sexual dimorphism in this paper).

1892. Ihering used the name *Peramys dimidiatus* for animals from Rio Grande do Sul.

1894. Figueira used the name "*Didelphys brevicaudata* Erxl." for Uruguayan *Monodelphis.*

1896. Lydekker wrote about *Didelphys dimidiata.*

1898. Holmberg recorded *Monodelphis dimidiata* from "La Tinta," Argentina, using the name "?*Didelphys brachyura*" (p. 478). Trouessart wrote about the geographic range of [*Peramys*] *dimidiata.*

1899. Lahille referred to *Peramys dimidiata* (Wagn.) as "El *Colicorto* de Azara.—Mesopotámica-orientalis.—Pampeana."

1900. Thomas reported *Peramys dimidiata* Wagn. from Palmeira, Parana, Brazil.

1914. Bertoni used the name *P* [*eramys*]. *dimidiatus,* stating that it was not "el ⟨⟨Colicorto⟩⟩ de *Azara.*"

1916. Matschie used the name combination "[*Didelphis* (*Monodelphis*)] *dimidiata* WAGN."

1919. Cabrera described the nominal genus *Minuania* with [*Minuania*] *dimidiata* Wagner as the type and only species. The distinguishing characters were largely those found (only?) in adult males.

1923. Larrañaga (1771–1848, published in 1923) referred to *D. Brachyura,* giving a description of external characteristics and some natural history notes. He considered it to be Azara's "*Colicorto.*"

1924. Thomas named *Monodelphis fosteri* from Caleufú, La Pampa, Argentina. Thomas compared *M. fosteri* with *M. dimidiata.*

1929. Sanborn recorded a specimen identified as *M. dimidiata* from Montevideo, Uruguay.

1932. Marelli used the combination *Minuania dimidiata.*

1935. Devincenzi used the combination *Minuania dimidiata* and put Azara's "*Colicorto*" in its synonymy.

1936. Miranda-Ribeiro described *P* [*eramys*]. *d* [*imidiata*]. *itatiayae* from Itatiaia, Rio de Janeiro, Brazil, and named *Minuania umbristriata* on page 422. On page 419, he included a key with the words: "[Coloração] ruiva, apparentemente uniforme . . . *M. goyana.*" *Minuania goyana* was mentioned only in the key. The description of *M. umbristriata* agrees with that of *M. goyana* in the key. Clearly, *M. goyana* and *M. umbristriata* were intended to apply to one and the same animal. In the key, two species were included in the subgenus *Minuania* (*M. dimidiata* and *M. goyana*). However, in the remainder of the paper, Miranda-Ribeiro recognized only *M. dimidiata* and *M. umbristriata* (see also Cabrera, 1958, below).

1939. Bertoni reported "*Peramys dimidiatus* (Wagn.)" from Puerto Bertoni, Alto Parana, Paraguay, and repeated that it is not "el ⟨⟨Colocorto⟩⟩ de Azara."

1940. Cabrera and Yepes gave the geographic range of *Minuania dimidiata* as Uruguay and Rio Grande do Sul to Rio de Janeiro, Brazil. They stated that this animal is not "el colicorto" of Azara, and recognized *Minuania umbristriata* Miranda-Ribeiro and *M. fosteri* (Thomas) as full species.

1941. Gilmore treated *Minuania* as a subgenus of *Monodelphis,* using color pattern as the criterion (but see Pine, 1976).

1955. Vieira wrote about *Monodelphis dimidiatus* (Wagner) and *Monodelphis umbristriata,* submerging *Minuania* in the synonymy of *Monodelphis.*

1958. Cabrera considered *Minuania goyana* Miranda-Ribeiro a *nomen nudum* and placed it in synonymy with *Monodelphis dimidiata.* He placed *Minuania umbristriata* in synonymy with *Monodelphis americana,* and treated *Minuania* as a subgenus of *Monodelphis,* containing *M. dimidiata* (Wagner) and *M. fosteri* Thomas.

1959. Lyne discussed the vibrissae in "*Peramys dimidiatus* Wagner," recording a specimen from "Palmeira, Parana, Brazil."

1960. Talice et al. wrote about the coloration and natural history of *Monodelphis dimidiata* in Uruguay. On pages 149 and 150, they seemed to think it likely that the "Colicorto" of Azara represented *M. dimidiata* but later (p. 152) contradicted this position.

1963. Godoy wrote that *M. fosteri* occurred in Buenos Aires and La Pampa in Argentina.

1964. Crespo reported on an animal identified by him as *Monodelphis* (*Minuania*) *fosteri* from Argentina. Reig felt that knowledge of the genus *Monodelphis* was not sufficient to justify recognition of the subgenus *Minuania.* He reported *M. dimidiata* from several localities in Argentina. He also stated that immature specimens of *M. dimidiata* have a coloration similar to that described by Thomas for *M. fosteri.* Reig suggested that *M. fosteri* Thomas may be a synonym of *M. dimidiata.*

1965. Reig wrote about the natural history of *M. dimidiata.* Fornes and Massoia compared specimens of Argentine *M. dimidiata* with those of typical Uruguayan *dimidiata* and found no differences (see also Massoia and Fornes, 1967).

1968. Avila Pires noted that the holotype of *P.* [*eramys*]. *d* [*imidiata*]. *itatiayae* Miranda-Ribeiro was, at that time, supposed to be prepared as a skin and skull. In the original description, the holotype was stated to be in alcohol. Avila Pires could not find the holotype in the Museu Nacional, Rio de Janeiro. He wrote that specimens from Itatiaia and Rio Grande do Sul could not be distinguished subspecifically. He followed Cabrera (1958) in treating *M. goyana* Miranda-Ribeiro as a synonym of *M. dimidiata,* also noting that he could not find the type (not realizing that *M. goyana* and *M. umbristriata* Miranda-Ribeiro are one and the same).

1969. Reig and Bianchi reported the karyotype of *M. dimidiata* from Argentina.

1972. Wainberg reported information concerning the karyotype of *M. dimidiata* from other localities in Argentina. Ximénez et al. gave information on the distribution of *M. dimidiata* in Uruguay. They also reported that Ximénez had examined the holotype of *M. d. itatiayae* and found no differences sufficient to justify subspecific distinction from *M. dimidiata* of Uruguay.

1974. Vaz-Ferreira and Palerm gave information on the natural history of *M. dimidiata* in Uruguay.

1975. Solari and Bianchi discussed the X and Y chromosomes of *M. dimidiata.*

1976. Pine treated *Minuania* as a valid subgenus containing *M. dimidiata* and *M. umbristriata.*

1977. Kirsch and Calaby did not recognize the subgenus *Minuania* and did not include *Monodelphis umbristriata* in their classification. They did, however, place *M. fosteri* in synonymy with *M. dimidiata,* based on the remarks made by Reig (1964).

1980. Pine compared the holotype of *P* [*eramys*]. *d* [*imidiata*]. *itatiayae* Miranda-Ribeiro with specimens of *M. henseli* from Brazil, and concluded that the former probably does not deserve subspecific recognition.

STATUS OF NAMED FORMS RELATED TO OR CONFOUNDED WITH *MONODELPHIS DIMIDIATA*

Monodelphis dimidiata (Wagner)

We have seen specimens of what C. O. Handley, Jr. (personal communication) regards as true *M. dimidiata* only from Argentina. This is unfortunate as the type locality is in Uruguay. Although we have not been able to make direct comparisons of the Brazilian specimens Handley identifies as *M. henseli* (probably a junior synonym of *M. sorex*) with the Argentine *M. dimidiata,* our recollections and notes indicate that the Brazilian specimens are more brightly colored on the flanks and belly, and darker dorsally than the Argentine ones. Bertoni (1914) also found what he regarded as northern (Paraguayan) *M. dimidiata* to be brighter than southern ones. Similarly, Cabrera and Yepes (1940, 1960) reported that specimens from the state of Rio de Janeiro, Brazil, were especially bright, and that for this reason they had been regarded as a separate subspecies. Reig (1964) noted that coastal Argentine *dimidiata* agreed in color with the type of *M. dimidiata,* and Massoia and Fornes (1967) also found them to essentially agree in color with Uruguayan specimens. However, Ximénez et al. (1972) reported that Ximénez had examined the holotype of *P* [*eramys*]. *d* [*imidiata*]. *itatiayae* (an *M. henseli* according to Handley) and found no differences justifying its separation at the subspecific level from topotypic *M. dimidiata.* They claimed that *M. dimidiata* shows variable coloration even at a single locality, which, by implication, could account for the external differences between the holotype of *itatiayae* and *M. dimidiata.*

As *M. dimidiata* has been confused with *M. henseli* (probably = *M. sorex*), the actual distributions of the two species and identities of some published specimens are problematical.

Monodelphis dimidiata itatiayae (Miranda-Ribeiro)

See *M. henseli.*

Monodelphis fosteri Thomas

This name was based on a single immature female from "Caleufú . . . about 64°30′W and 35°35′S . . . La Pampa, Argentina." Thomas (1924) wrote, "This specimen is just about the same age as a number of *M. dimidiata* which I collected in 1896 near Montevideo, and is conspicuously different in colour from any of them," describing *M. fosteri* as "of a very much paler grey colour above, near 'deep mouse-grey,' the sides scarcely more buffy than the back, the belly only faintly tinged with buffy, as is also the case with the cheeks, instead of these parts being in each case strong prominent buffy. Tail bicolor, black above, whitish below. Skull and teeth as in *dimidiata.*"

Reig (1964) stated that his immature *M. dimidiata* from Argentina had the coloration Thomas gave for *fosteri,* being paler than Reig's adults and the holotype of *M. dimidiata.* This seems odd because the specimens from Balcarce, which is not far from Reig's localities, show the reverse, the young being darker than the adults, as was also reported by Crespo (1964) for his Argentine *Monodelphis.* Our notes taken on one of three essentially identical immature male specimens from Balcarce (MSU 17469), with total length equals 120 mm, skull equals 23.5 mm ("age group 3"), are as follows: "belly fur . . . with gray bases tipped with buff [;] belly much darker than in adults which have more or less monochromatic orangish or yellowish bellies. Lateral orangish color on flanks not nearly as well-developed as in adults. Side of head and neck fairly orange however." These immatures are darker and browner overall than the adults. One point apparently missed by Reig is that Thomas (1924) compared the (pale) type of *M. fosteri* with what he regarded as typical (dark) *M. dimidiata* of approximately the same age. Assuming Thomas' *M. fosteri* shows a growth pattern similar to that of *M. dimidiata* from near Balcarce, its holotype would, judging from its measurements, fall in our "age group 5," at which time adult pelage should be developed (as Thomas no doubt knew). Reig, however, concluded that *M. fosteri* Thomas is probably a synonym of *M. dimidiata,* with *M. fosteri*'s characters being merely those typical of juvenile *dimidiata.* He made no definite decision on this, however, and stated that his supposition ought to be checked out by comparison of types and study of specific characters in the genus. According to Kirsch and Calaby (1977), however, "Reig (1964) showed that *M. fosteri* specimens were simply juveniles of *M. dimidiata,* and *fosteri* is accordingly omitted [from their list of species]." Although they have not themselves made the studies recommended by Reig, Kirsch and Calaby have treated the conspecificity of *M. dimidiata* and *M. fosteri* as proved and they were the first to place the names in synonymy. We believe that the conservative course is to treat *M. fosteri* as a full species pending further direct comparisons with other specimens.

Monodelphis goyana (A. de Miranda-Ribeiro)

See *M. umbristriata.*

Monodelphis henseli (Thomas)

This name is a junior synonym of *Monodelphis sorex* (Hensel) according to C. O. Handley, Jr. (personal communication). Handley has convinced us that the holotype of *P* [*eramys*]. *d* [*imidiata*]. *itatiayae* Miranda-Ribeiro is a junior synonym of *M. henseli* (see Pine, 1980).

Monodelphis sorex (Hensel)

See *M. henseli.*

Monodelphis umbristriata (Miranda-Ribeiro)

In the same paper (p. 422) as the description of "*Monodelphis dimidiata itatiayae,*" Miranda-Ribeiro (1936) named *Minuania umbristriata.* On page 419 in a key, he wrote, "[Coloracão] ruiva, apparentemente uniforme . . . *M. goyana.*" Cabrera (1958) tentatively placed *Minuania umbristriata* in the synonymy of *Monodelphis americana*

Müller. In regard to *M. goyana,* Cabrera wrote "mencionada solamente en una clave, sin indicación de localidad ni más caracteres diferenciales que . . . [quotes Miranda-Ribeiro], apenas puede ser considerada más como un *nomen nudum.* En todo caso, es por ahora una forma nominal muy dudosa, tal vez simplemente una variante erítrica de *dimidiata.*" Brief as Miranda-Ribeiro's remarks are, they constitute a description, and whatever *M. goyana*'s status, it is not a *nomen nudum.* Although this did not occur to Cabrera, it is clear that *Minuania goyana* and *Minuania umbristriata* were intended to apply to one and the same animal. In his key, Miranda-Ribeiro recognized two species in the subgenus *Minuania* (*M. dimidiata* and *M. goyana*). In the rest of the text, he also recognized two species (*M. dimidiata* and *M. umbristriata*). The description of *M. goyana* in the key agrees with the description of *M. umbristriata* in the main text. The specific name *goyana* in Brazilian Portuguese means a (female) inhabitant of the Brazilian state Goiás, and both of Miranda-Ribeiro's specimens of *M. umbristriata* are from that state. Obviously, he initially intended to call his new form by one name and then changed his mind but failed to make all the necessary changes in his manuscript. As first revisers, we select the name *Minuania umbristriata* Miranda-Ribeiro 1936 to have priority over *Minuania goyana* Miranda-Ribeiro 1936.

Pine (1976) reported a specimen of *Monodelphis umbristriata* from Minas Gerais, and treated *Minuania* as a valid subgenus containing *M. umbristriata* and *dimidiata.* A character used by Miranda-Ribeiro (1936) and Pine (1976) to distinguish *M. umbristriata* (as adults) from other striped-backed *Monodelphis* was the extremely faint dorsal stripes in *M. umbristriata.* Thomas (1888) noted this color pattern in animals he called *M. americana* and remarked that it may be seasonal because he had seen a specimen in Paris that was rufous-striped anteriorly and black-striped posteriorly. When Miranda-Ribeiro (1936) and Pine (1976) were writing about *M. umbristriata,* the extreme sexual dimorphism in at least some *Monodelphis* was unappreciated. The status of the name *M. umbristriata* may be in need of reassessment because both reported adult specimens are males.

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ON THE GENUS *SIERROBIUS* STRANEO, 1951 (COLEOPTERA: CARABIDAE: PTEROSTICHINI)

Stefano L. Straneo[1]

Abstract

The genus *Sierrobius* Straneo, 1951, and its subgenus *Pachyabaris* Straneo, 1951, are peculiar to the Sierra Nevada de Santa Marta, Colombia. Three of the species attributed in the original description to *Pachyabaris* (*laevis* Straneo, 1951, *minuta* Straneo, 1951, and *striolata* Straneo, 1951) are better placed in *Sierrobius* (*Sierrobius*) (new combinations). Four new species of subgenus *Sierrobius* are described here: *kochalkai, davidsoni, aberrans,* and *angularis.* Of these species, *angularis* and *aberrans* have a shape rather different from the other species of subgenus *Sierrobius* and probably require a new subgenus.

Introduction

I described the genus *Sierrobius* in 1951 for five new species from Colombia, Sierra Nevada de Santa Marta, sent to me for determination by my friend Dr. P. J. Darlington, Jr., of the Museum of Comparative Zoology, Harvard University, where the holotypes are deposited. Each of these species (with a single exception) was represented by a single specimen. In the same paper, I described also the new genus *Pachyabaris,* with five new species also from Sierra Nevada de Santa Marta—four of these species represented by one to four specimens, the fifth by

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10 specimens. I later (Straneo, 1977, 1979) became convinced that *Pachyabaris* was no more than a subgenus of *Sierrobius. Sierrobius* and *Pachyabaris* are, as far as I know, peculiar to the Sierra Nevada de Santa Marta. I have not yet seen any other species from other localities assignable to these two subgenera.

Some months ago, Robert L. Davidson of the Carnegie Museum of Natural History sent to me for determination a collection of 23 specimens belonging to the genus *Sierrobius,* which were collected in the Sierra Nevada de Santa Marta by his friend, John A. Kochalka. Among these specimens I found five of the previously described species and four new very well defined species. The study of this important material convinced me that only the species *darlingtoni* and *subcordatus* should be separated from the true *Sierrobius* by the wholly different general shape and remain in the subgenus *Pachyabaris.* The three other species formerly placed there (*laevis, minuta,* and *striolata*) are better placed in *Sierrobius* (*Sierrobius*) (NEW COMBINATIONS).

CHECKLIST OF THE SPECIES OF *SIERROBIUS*

Sierrobius (*Sierrobius*) *laevis* (Straneo, 1951), new combination
Sierrobius (*Sierrobius*) *minutus* (Straneo, 1951), new combination
Sierrobius (*Sierrobius*) *striolatus* (Straneo, 1951), new combination
Sierrobius (*Sierrobius*) *kochalkai,* new species
Sierrobius (*Sierrobius*) *davidsoni,* new species
Sierrobius (*Sierrobius*) *aberrans,* new species
Sierrobius (*Sierrobius*) *angularis,* new species
Sierrobius (*Sierrobius*) *smaragdinus* Straneo, 1951
Sierrobius (*Sierrobius*) *laevigatus* Straneo, 1951
Sierrobius (*Sierrobius*) *bistriatus* Straneo, 1951
Sierrobius (*Sierrobius*) *uniformis* Straneo, 1951
Sierrobius (*Sierrobius*) *parvulus* Straneo, 1951
Sierrobius (*Pachyabaris*) *darlingtoni* (Straneo, 1951), new combination
Sierrobius (*Pachyabaris*) *subcordatus* (Straneo, 1951), new combination

Genus ***Sierrobius*** Straneo, 1951

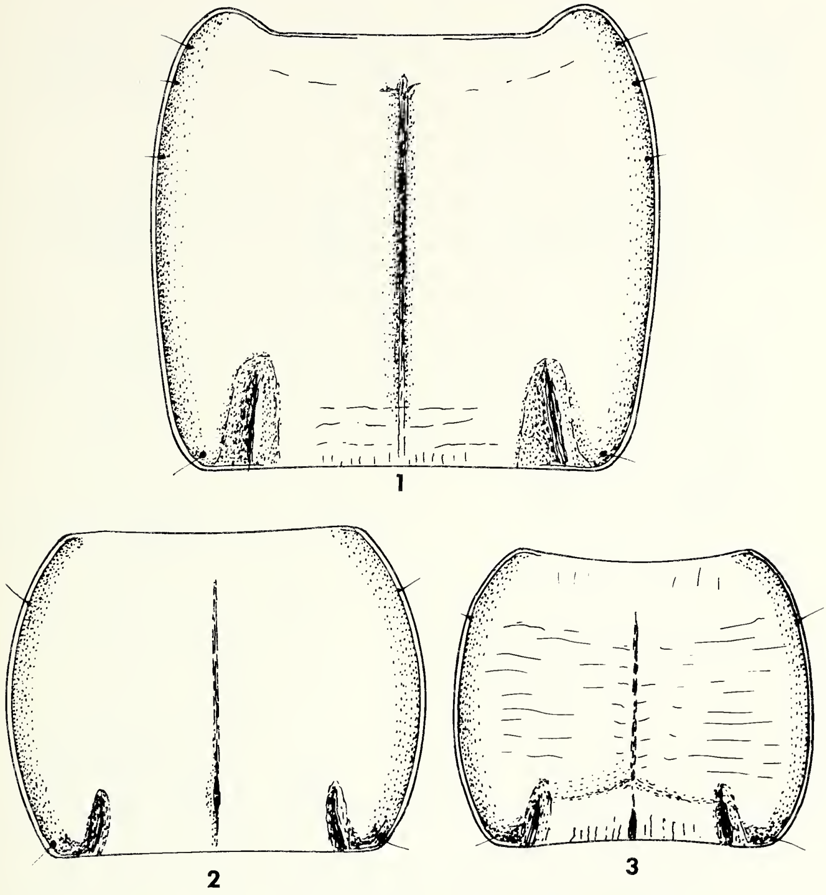
Subgenus ***Sierrobius*** Straneo, 1951

Type species.—*Sierrobius smaragdinus* Straneo, 1951, by original designation.

Subgenus ***Pachyabaris*** Straneo, 1951, new status

Type species.—*Pachyabaris darlingtoni* Straneo, 1951, fixed here.

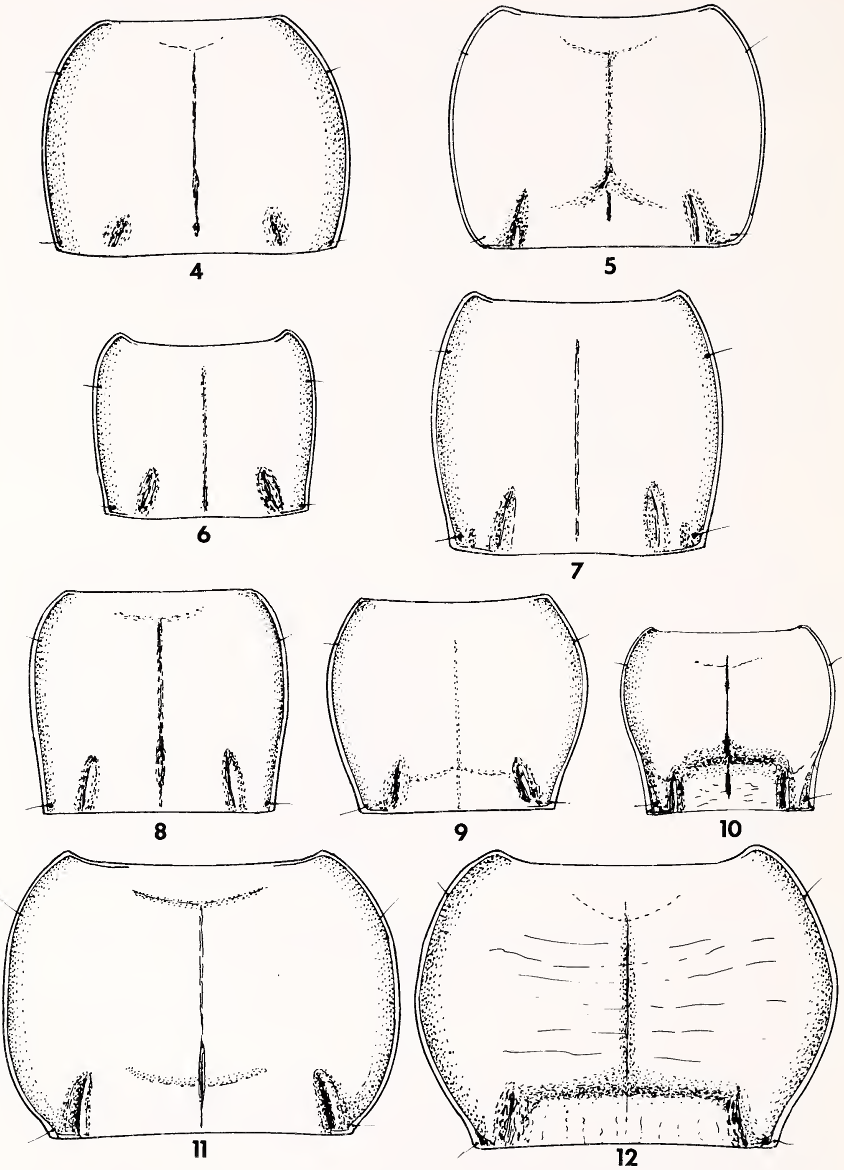
This genus belongs to the tribe Pterostichini. The chief characters of the genus are: paraglossae without setae at their extremities; antennae average, elongate, antennomeres 4–10 distinctly longer than wide; elytra normally striate, intervals smooth, regular; crossing of epipleura



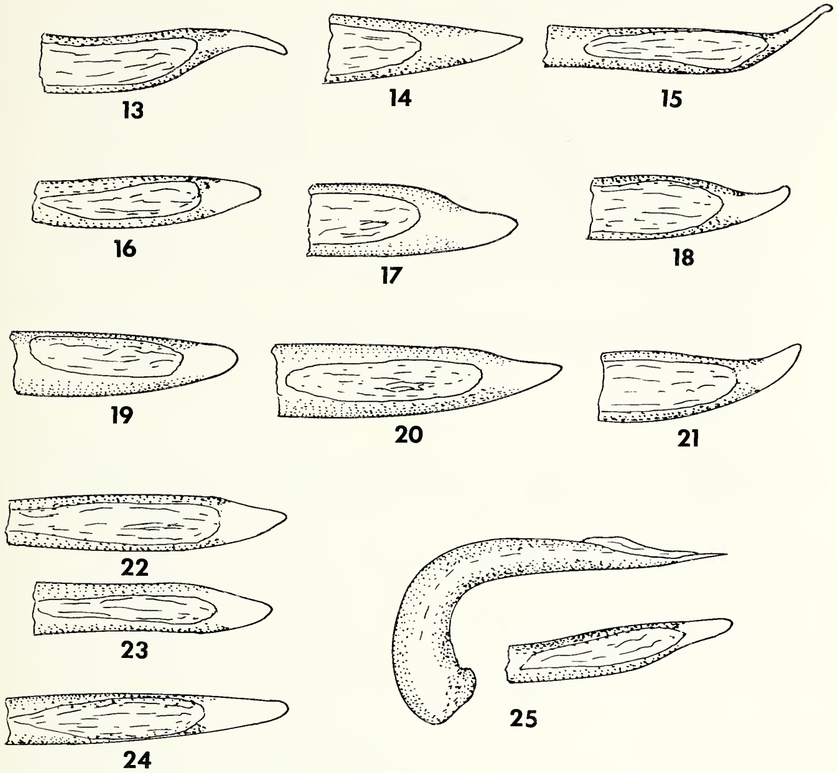
Figs. 1–3.—Sketches of the shape of pronotum of some species of *Sierrobius*. 1. *S. smaragdinus*; 2. *S. bistriatus*; 3. *S. kochalkai*.

well developed; third interval with 3 punctures; sterna IV-VI entirely transversely sulcate (or nearly so) and margined basally, transverse sulcus with large and deep punctures.

Owing to the kindness of the authorities of the Museum of Comparative Zoology, I was able to see again the types of the previously described species not represented in my collection by paratypes, so that I am able to present a key to the species of the genus *Sierrobius*.



Figs. 4–12.—Sketches of the shape of pronotum of some species of *Sierrobius*. 4. *S. laevis*; 5. *S. davidsoni*; 6. *S. minutus*; 7. *S. striolatus*; 8. *S. parvulus*; 9. *S. aberrans*; 10. *S. angularis*; 11. *S.* (*Pachyabaris*) *darlingtoni*; 12. *S.* (*Pachyabaris*) *subcordatus*.



Figs. 13–25.—Sketches of the shape of apical blade of aedeagus (dorsal view) of some *Sierrobius*. 13. *S. smaragdinus*; 14. *S. laevigatus*; 15. *S. bistriatus*; 16. *S. kochalkai*; 17. *S. laevis*; 18. *S. davidsoni*; 19. *S. minutus*; 20. *S. striolatus*; 21. *S. parvulus*; 22. *S. aberrans*; 23. *S. angularis*; 24. *S.* (*Pachyabaris*) *darlingtoni*. 25. Sketch of the shape of aedeagus of *Sierrobius* (*Pachyabaris*) *subcordatus*, lateral view and dorsal view.

KEY TO THE ADULTS OF THE SPECIES OF THE GENUS *SIERROBIUS*

1(0). Pronotum subrectangular or subtrapezoidal (Figs. 1–10), sides little rounded; base little narrower than greatest width (if sides sinuate before base and base narrower, then size smaller, length 7–8 mm). *Sierrobius* (*sensu stricto*) 2

1′. Pronotum with sides strongly rounded (Figs. 11–12); base much narrower than greatest width; part of pronotum between basal impressions moderately or rather strongly depressed; length 9–11 mm. *Sierrobius* (*Pachyabaris*) .. 13

2(1). Size greater than 10 mm; base of pronotum between basal impressions continuing the convexity of the disc 3

2′. Size smaller, generally less than 8 mm; base of pronotum between basal impressions either continuing the convexity of the disc or flat 7

3(2). Anterior half of lateral border of pronotum with 2–3 setigerous pores; color of upper surface bright metallic green, shiny (Fig. 1); apical blade of aedeagus as in Fig. 13 ... *smaragdinus* Straneo

3′. Anterior half of lateral border of pronotum with only the usual single setigerous pore ... 4

4(3′). Elytral striae more or less faint, except seventh, which is always rather deeply impressed; upper surface always with strong metallic reflections ... 5

4′. All elytral striae uniformly and rather deeply impressed; upper surface without or with faint metallic reflections ... 6

5(4). Length 16 mm; elytra entirely smooth; upper surface violaceous red with some greenish reflections; apical blade of aedeagus nearly symmetrical (Fig. 14) ... *laevigatus* Straneo

5′. Length about 12 mm; elytra with striae 3 and 4 more or less evident; upper surface bright, various—head and pronotum dark blue and elytra blue-green or uniformly bright bronze or copper bronze; apical blade of aedeagus strongly asymmetrical (Fig. 15); pronotum as in Fig. 2 ... *bistriatus* Straneo

6(4′). Length 14 mm; scutellary stria without basal pore; color brown ... *uniformis* Straneo

6′. Length 11 mm; scutellary stria with basal pore; color blackish, lateral border of elytra and pronotum reddish; first puncture of third interval adjoining third stria; pronotum as in Fig. 3; apical blade of aedeagus as in Fig. 16 ... *kochalkai,* new species

7(2′). Sides of pronotum moderately but evidently rounded for the entire length (Figs. 4 and 5) ... 8

7′. Sides of pronotum very little rounded in the anterior half and nearly straight or subsinuate toward base (Figs. 6–10) ... 9

8(7). Color bright bronze; basal angles of pronotum not rounded, slightly blunt in some specimens; space between basal impressions of pronotum not depressed; basal impressions very short, not reaching base (Fig. 4); apical blade of aedeagus as in Fig. 17 ... *laevis* (Straneo)

8′. Color not or very faintly metallic; basal angles of pronotum rounded; space between basal impressions moderately but evidently depressed; basal impressions longer and reaching base; first and second punctures of third interval adjoining third stria; pronotum as Fig. 5; apical blade of aedeagus as in Fig. 18 ... *davidsoni,* new species

9(7′). Sides of pronotum straight toward base; space between basal impressions and hind angles convex (Figs. 6–8); color bronze ... 10

9′. Sides of pronotum gently but evidently subsinuate (Figs. 9 and 10); color blackish brown without metallic reflections ... 12

10(9). All striae of elytra entire and well developed; anterior impressed puncture of third interval adjoining third stria, the other two adjoining second stria 11

10′. Striae in part faint; two anterior punctures of third interval adjoining second stria; pronotum as in Fig. 6; apical blade of aedeagus as in Fig. 19 ... *minutus* (Straneo)

11(10). Pronotum more transverse (ratio length/width about 0.78); striae of elytra more deeply impressed; punctures of third interval moderate as usual; pronotum as in Fig. 7; apical blade of aedeagus as in Fig. 20 ... *striolatus* (Straneo)

11′. Pronotum more elongate (ratio length/width about 0.90, Fig. 8); striae of elytra in the posterior half very shallow; punctures of the third interval larger than usual, more or less foveate; apical blade of aedeagus as in Fig. 21 ... *parvulus* Straneo

12(9′). Prebasal subsinuosity of sides of pronotum very faint; pronotum less narrowed towards base; hind angles not raised (Fig. 9); slightly larger (length 7.8 mm); apical blade of aedeagus narrower and more elongate (Fig. 22) .... *aberrans*, new species

12′. Prebasal subsinuosity of sides of pronotum more evident; pronotum more narrowed towards base; basal angles distinctly raised so that basal impressions look wider and deeper (Fig. 10); slightly smaller (length 7 mm); apical blade of aedeagus less narrow and less elongate (Fig. 23) .... *angularis*, new species

13(1′). Sides of pronotum strongly rounded nearly to base; basal angles very short (Fig. 11); apical blade of aedeagus as in Fig. 24 .... *darlingtoni* (Straneo)

13′. Sides of pronotum strongly sinuate before basal angles, which are not rounded (Fig. 12); apical blade of aedeagus as in Fig. 15 ..... *subcordatus* (Straneo)

DESCRIPTIONS OF NEW SPECIES AND ADDITIONAL DATA ON CURRENTLY RECOGNIZED SPECIES

***Sierrobius* (*Sierrobius*) *kochalkai*,** new species

Specimens examined.—2.

Holotype.—Carnegie Museum of Natural History, Holotype Number 798, male, labelled: Colombia, Sierra Nevada de Santa Marta, Rio Donachui, 13,200 ft (4023 m) (J. A. Kochalka 4.I.1973).

Paratype.—Coll. Straneo, male: same locality and data.

Description.—Length 10 mm; greatest width 3.3 mm. Head and pronotum dark brown, rather shiny, with lateral margin of pronotum reddish; elytra black with faint greenish reflection, not shiny, slightly sericeous; antennae and legs completely ferrugineous.

Head moderately elongate with two supraorbital setae; eyes rather little convex; temples no longer than one-half length of eye; frontal impressions deep, very short, not reaching level of anterior supraorbital pore; front between impressions moderately convex, smooth.

Pronotum (Fig. 3) transverse; anterior margin nearly straight; sides rather rounded anteriorly, then little rounded to basal angles, which are rounded; lateral border very narrow, linear, with two usual setae, posterior one on basal angle; basal impressions deep, little divergent behind; space between impressions and basal angles moderately convex; base nearly straight, evidently depressed between impressions; disc little convex, median longitudinal line rather deep, reaching base, strongly deepened and subfoveate behind; pronotum with some small longitudinal impressed lines laterally and some undulating transverse lines on the disc at the sides of the median line.

Elytra subparallel-oval, with strong isodiametric microsculpture (meshes transverse, nearly 1.5 times longer than wide); basal border strong and entire, obtusely joined to lateral margin with sharp angle; shoulders rounded; sides moderately divergent behind shoulder, with greatest width at ⅓ length, thence nearly parallel for ⅓ length, then rounded to apex; preapical sinuosity well developed; striae deep, faintly crenulate; scutellary stria well developed; basal pore very small, at the junction of scutellary and second stria; interstices very little convex, third one with 3 punctures, anterior puncture at ¼ length and joining third stria, second puncture at ⅔ length and nearly interrupting the interstice, last puncture about ⅔ of the distance from second puncture to apex; crossing of epipleurae well marked; umbilicate series not interrupted at middle and including about 16 pores.

Legs normal; posterior tarsi not grooved laterally; last tarsomere with some setae ventrally. Prosternum not grooved or impressed longitudinally; prosternal process strongly margined, chiefly laterally; proepisterna smooth, impunctate. Metepisterna trapezoidal, lateral border a little longer than anterior border, not margined, impunctate. Abdominal sterna with transversely punctate groove, as usual in *Sierrobius*; last sternum simple, with 1+1 (male) or 2+2 (female) setigerous punctures. Aedeagus with apical blade as in Fig. 16.

Etymology.—This species is dedicated to John A. Kochalka, collector of the interesting material which allowed me to make the present study.

***Sierrobius* (*Sierrobius*) *davidsoni*, new species**

Specimens examined.—2.

Holotype.—Carnegie Museum of Natural History, Holotype Number 797, male, labelled: Colombia, Sierra Nevada de Santa Marta, Lake Arucuina, Rio Tucurinca 13,700 ft (J. A. Kochalka 12.III.1975).

Allotype.—Coll. Straneo, female: same locality and data.

Description.—Length 8.2 mm; greatest width 2.8 mm. Upper surface brown with faint metallic reflection; lateral border of pronotum reddish; underside, antennae, and legs ferrugineous brown.

Head rather elongate, with two usual supraorbital punctures; eyes not wide, very moderately convex; temples very short, inconspicuous; frontal impressions, deep, short, not reaching the level of anterior supraorbital seta; front between impressions smooth, convex.

Pronotum subrectangular (Fig. 5); anterior margin little excavated; anterior angles rounded, not prominent; sides very gently rounded in middle, more strongly so anteriorly and posteriorly, greatest width a little before middle; lateral border narrow, thin, with two usual setae, posterior one on the basal angle, which is rounded; basal impressions rather narrow, deep, elongate, reaching base; space between impressions and basal angle little convex, as is the disc; median line deep, shortened anteriorly and posteriorly; base straight, with a thin margined border from angles to basal impressions, a little depressed between them.

Elytra elongate, ovate, with strong isodiametric microsculpture (but shallower than in *kochalkai*); length 4.7 mm, greatest width 2.8 mm near middle; basal border entire, joining lateral border nearly at right angle; shoulders a little angular; sides moderately rounded for whole length; preapical sinuosity and crossing of epipleurae rather strong; scutellary stria very short or effaced; striae in basal third well defined, though sometimes only by a series of superficial small punctures, thence nearly effaced; intervals completely flat, third one with three punctures, anterior puncture at ⅕ length, second and third at ⅔ and ⅘ length, first and second ones adjoining third stria, third one adjoining second stria; umbilicate series composed of 8+1+6 pores.

Prosternum with moderately deep longitudinal impression in basal half; prosternal process flat with faint vestigial border visible only with oblique light; proepisterna smooth, impunctate. Metepisterna with lateral border a little longer than anterior border. Abdominal sterna with transverse punctate groove, as usual in *Sierrobius*; last sternum with 1+1 (male) and 2+2 (female) setigerous punctures. Aedeagus as in Fig. 18.

The shape of the pronotum in this species is similar to that of *kochalkai,* but the sides are still less rounded, the disc is shiny and there are no undulating transverse lines. The depression between basal impressions is very faint. Two punctures of the third interval adjoin the third stria (instead of only the first one as in *kochalkai*).

Etymology.—This species is dedicated to Robert L. Davidson, who loaned me this interesting material.

Sierrobius* (*Sierrobius*) *aberrans, new species

Specimens examined.—2.

Holotype.—Carnegie Museum of Natural History, Holotype Number 799, male, labelled: Colombia, Sierra Nevada de Santa Marta, Lake N. of P. Norte Grande, Serra Donan Chucua 13,100 ft (J. A. Kochalka, 7.III.1975).

Allotype.—Coll. Straneo, female, labelled: Colombia, Sierra Nevada de Santa Marta, lake, Rio Donachui 14,400 ft (J. A. Kochalka, 8.I.1973).

Description.—Length 7.8–8.2 mm; greatest width 2.8–3.0 mm. Upper surface dark brown, shiny; elytra nearly as shiny as head and pronotum (due to very shallow microsculpture); underside, legs, and antennae ferrugineous brown, rather dark.

Head rather elongate, with two usual supraorbital setae on each side; eyes moderately convex; temples as convex as eyes, shorter than ½ length of eye; frontal impressions deep, nearly reaching level of first supraorbital seta; front between impressions convex.

Pronotum subtrapezoidal (Fig. 9), little convex, anteriorly very little emarginate; sides uniformly rounded for ⅔ length, thence straight or slightly subsinuate, converging to base; greatest width at ⅗ length from base; anterior angles rather acute, a little prominent; basal angles nearly square, with apices not rounded and not raised; lateral border narrow, thin, surrounding basal angles and forming a short very narrow basal border; basal impressions rather deep, short, not reaching base; space between impressions and basal angles moderately convex, as is the disc; median line deep, narrow, reaching base, which is a little depressed between impressions.

Elytra oval, very moderately convex, nearly 1.55 times longer than wide; microsculpture isodiametric, very shallow and dense; base bordered; shoulders obtuse, not rounded; sides strongly rounded behind base, then less rounded, with greatest width at ⅗ length; preapical sinuosity well developed; all striae well impressed, nearly smooth; scutellary stria variable, in the holotype well impressed on one elytron, less so on the other; basal pore at base of second stria indistinct; intervals little convex, even near apex; third interval with 3 punctures, anterior one at ⅕ length and adjoining third stria, second and third punctures at ⅔ and ⅘ length; umbilicate series beginning rather far back from shoulders and consisting of 3+1+1+7 pores.

Legs normal; last tarsomere with several setae ventrally. Proepisterna smooth. Metepisterna a little longer than wide, strongly narrowed posteriorly, with a partial strong groove on medial side. Abdominal sterna with transverse punctate grooves less developed than is usual in *Sierrobius*; last sternum with 1+1 (male) or 2+2 (female) setigerous punctures. Apical blade of aedeagus narrow and rather elongate (Fig. 22).

The trapezoidal shape of the pronotum, the weakly convex pronotum and elytra, and the lack of any metallic reflection give to this species and to the following one an appearance rather different from usual *Sierrobius*. It is possible that they should be placed in a new subgenus.

Sierrobius **(*Sierrobius*)** ***angularis***, new species

Specimens examined.—4.

Holotype.—Carnegie Museum of Natural History, Holotype Number 800, male, labelled: Colombia, Sierra Nevada de Santa Marta, Plateau pond on north branch of Quebrada Silvestre 13,950 ft (4251 m), 9.III.1975 (J. A. Kochalka).

Allotype.—Coll. Straneo, female: same locality and data.

Paratypes.—Carnegie Museum of Natural History and Coll. Straneo, two females, labelled: Colombia, Sierra Nevada de Santa Marta, lake, Rio Tucurinca 4785 m, 16.III.1975 (J. A. Kochalka).

Description.—Length 7 mm; greatest width 2.5 mm. Upper surface brown, without any metallic reflections; head and pronotum shiny, elytra a little less so in male, dull sericeous in the female due to stronger microsculpture; underside, legs, and antennae ferrugineous brown.

Head moderately elongate, with two usual supraorbital setae on each side; eyes rather wide and convex; temples as long as ½ eye length; frontal impressions deep, rather wide, reaching the level of anterior supraorbital seta; front between impressions moderately convex, smooth.

Pronotum subtrapezoidal (Fig. 10), moderately convex; anteriorly little emarginate; anterior angles not prominent, rounded; sides strongly rounded for ⅔ length, thence straight or slightly subsinuate, converging to base; lateral border very narrow, linear, with two usual setigerous punctures, basal one a little inside and a little advanced from basal angle; basal angles nearly rectangular, raised, not blunt; basal impressions deep, wide, seemingly wider and deeper because of the raised basal angles; space between impressions and basal angles concave; base nearly straight, with faint vestigial border at sides; median line more or less deep, irregularly widened in some places, shortened anteriorly, not reaching base.

Elytra subparallel-oval, nearly 1.6 times longer than wide; microsculpture isodiametric, shallow and dense in the male, much stronger in the female; base bordered; shoulders moderately obtuse, a little angular; sides moderately rounded, greatest width nearly at middle; all striae deep; scutellary stria short, variable, sometimes faint; basal pore indistinct; intervals moderately convex, third interval with 3 punctures, anterior puncture at ⅕ length and adjoining third stria, two others at ⅔ and ⅘ length and adjoining second stria; umbilicate series of 5+1+7 pores; preapical sinuosity well developed.

Prosternum with short longitudinal depression; prosternal process strongly depressed so that it appears to have a false border; proepisterna smooth. Metepisterna a little longer than wide, strongly narrowed posteriorly. Abdominal sterna with punctate groove interrupted at middle. Aedeagus as in Fig. 23.

Sierrobius* (*Sierrobius*) *parvulus Straneo, 1951

Specimens examined.—3.

Holotype.—Museum of Comparative Zoology, Harvard University, Type Number 28,429, female, labelled: Colombia, Northwestern Sierra Nevada de Santa Marta, 8–11,000 ft (Feb. 10–12, 1929, Darlington).

Additional material examined.—Colombia, Sierra Nevada de Santa Marta, Cuch. Cebolleta, 3505 m (J. A. Kochalka, 9 May 1975). 2 specimens (Carnegie Museum of Natural History, Coll. Straneo).

Remarks.—This species was described from a single female. As one of the Kochalka specimens is a male, I have included a sketch of the apical blade of the aedeagus (Fig. 21).

Sierrobius* (*Sierrobius*) *laevis
(Straneo, 1951), new combination

Holotype.—Museum of Comparative Zoology, Type Number 28,431, male, labelled: Colombia, N.W. Sierra N. de Sta Marta, 11–12,000 ft (Darlington, 10–12.II.1929).

Additional material examined.—Colombia, Sierra Nevada de Santa Marta, Cuch. Cebolleta, 3505 m. (J. A. Kochalka, 9 May 1975). 2 specimens (Carnegie Museum of Natural History, Coll. Straneo).

***Sierrobius* (*Sierrobius*) *bistriatus* Straneo, 1951**

Holotype.—Museum of Comparative Zoology, Type Number 28,428, male, labelled: Colombia, N.W. Sierra N. de Sta Marta, 8–11,000 ft (Darlington, 10–11.II.1929).

Additional material examined.—Colombia, Sierra Nevada de Santa Marta, Casa Antonio, Loma Cebolleta, 2700 m (J. A. Kochalka, 8 May 1975). 2 specimens (Carnegie Museum of Natural History, Coll. Straneo).

Sierrobius* (*Pachyabaris*) *darlingtoni
(Straneo, 1951), new combination

Holotype.—Museum of Comparative Zoology, Type Number 28,433, male, labelled: N.W. Sierra N. de Sta Marta, 12,000 ft (Darlington, 11.II.29).

Allotype.—Coll. Straneo, female, same locality and data.

Paratype.—Museum of Comparative Zoology, female, same locality and data.

Additional material examined.—Colombia, Sierra Nevada de Santa Marta, S. of lake branch Que. el Chorro, 3797 m (J. A. Kochalka, 5 February 1975). 3 specimens (Carnegie Museum of Natural History, 2, Coll. Straneo).

Sierrobius* (*Pachyabaris*) *subcordatus
(Straneo, 1951), new combination

Specimens examined.—5.

Holotype.—Museum of Comparative Zoology, Type Number 28,435, female, labelled: Colombia, Sierra Nevada de Santa Marta, 12,000 ft, Feb. 11, 1929 (Darlington).

Additional material examined.—Colombia, Sierra Nevada de Santa Marta, 3797 m, S. of lake branch Que. el Chorro (J. A. Kochalka, 5 March 1975). Lake N. of P. Norte Grande, Serr. Donan Chucua, 13,100 ft (J. A. Kochalka, 7 March 1975). 4 specimens (Carnegie Museum of Natural History, 2, Coll. Straneo, 2).

Remarks.—This species too was described from an unique female specimen. In Fig. 25, I give a sketch of the apical blade and left lateral aspect of the aedeagus.

RESUME

Le genre *Sierrobius* Straneo 1951 et son sousgenre *Pachyabaris* Straneo 1951 se rencontrent exclusivement sur la Sierra Nevada de Santa Marta, Colombia. Trois des espèces attribuées dans la description originale à *Pachyabaris* sont mieux placées dans *Sierrobius* (*Sierrobius*) (*laevis* Straneo, 1951, *minuta* Straneo, 1951, *striolata* Straneo, 1951). Quatre *Sierrobius* nouveaux (*kochalkai, davidsoni, aberrans, angularis*) sont décrits ici. Les deux dernières espèces (*aberrans, angularis*) ont un faciès particulier et devront probablement être placées dans un sousgenre nouveau.

ACKNOWLEDGMENTS

I am very grateful to Robert L. Davidson for the communication of this very interesting material and for the duplicates generously presented to my collection. I would like to thank the authorities of the Museum of Comparative Zoology for the loan of all the unique types of this genus.

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ADDITIONAL NOTES ON THE CLASSIFICATION AND KNOWLEDGE OF STINGLESS BEES (MELIPONINAE, APIDAE, HYMENOPTERA) BY THE KAYAPÓ INDIANS OF GOROTIRE, PARÁ, BRAZIL[1]

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Abstract

This work presents additional data regarding the knowledge of meliponines by the Gorotire-Kayapó Indians of Brazil. Factors determining the Indian taxonomic system for stingless bees include: habitat; preferred substrate or niche; external nest form; texture, material, and shape of entrance structure; flight patterns; defense behavior; size, form, and color of adults; and smell of bees. Detailed ethnobiological descriptions of the following species are included: *Tetragona clavipes, Partamona* cf. *cupira, Scaptotrigona*

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[1] This work is the result of one phase of the Projecto Kayapó, an interdisciplinary project to study the ethnobiology of the Kayapó Indians, financed by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and the World Wildlife Fund–U.S. The entire project involves 14 scientists from different fields of expertise and is conducted by the Laboratório de Etnobiologia, Universidade Federal do Maranhão, São Luís, MA, Brazil.

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Submitted 22 March 1984.

polystica, Melipona rufiventris flavolineata, Melipona melanoventer, Tetragonisca angustula angustula, Tetragona dorsalis cf. *beebei, Trigona fulviventris.* Indigenous concepts of ontogeny, division of labor, castes, odor trails, defense activity, swarming, and general behavior are discussed. Bee management, or "semi-domestication," methods of collection, and use of bees' wax, cerumen, resin, pollen, larvae, and honey are discussed. Suggestions for future research generated from this ethnobiological investigation include: use of chemical properties (odors) in species identification; division of labor within bee colonies; generation of odor trails by Trigonini; symbiotic relationships between acarine mites and meliponines; habitat sharing and specificity; and the role of *Apis mellifera* in the modification of stingless bee behavior. The work concludes with a discussion of the symbolic importance of bees to the Gorotire-Kayapó as "natural models" for social organization and the importance of ethnobiological research in the creation of a world science.

INTRODUCTION

Initial research by Posey (1983*e*) recorded 56 named folk species of stingless bees that are recognized and classified by the Kayapó Indians from the village of Gorotire (7°48'S, 51°7'W) in the Brazilian state of Pará. Of these, nine species are considered "semi-domesticated" or "manipulated" by the Indians.

Many of these meliponine bees are of economic importance to the Kayapó. Wax, cerumen, and resin are used for artifacts; honey, pollen, and larvae are used for food; pupae are used for food and medicine; and pollen and bee parts are important in medicinal preparations (Posey, 1983*e*). Even nonutilitarian species are known and classified by the Kayapó, who consider all social insects to be of epistemological importance. The Indians believe that an ancient shaman (*wayanga*), who studied social *Hymenoptera* behavior, taught their ancestors how to live, work, and defend themselves like social insects (Posey, 1983*f*). This "natural model" for society is symbolically represented by the nests of *Polybia* spp. wasps (*amuh*) and ceremonially manifested in a special meliponine beeswax (cerumen) hat called mẽkutôm (Posey, 1983*c*, 1983*d*).

This paper presents additional data on the complex knowledge of the Kayapó Indians to further document the folk science of these extraordinary experts on Amazonian biology and ecology. Our intent is not to compare our science with theirs, but rather to show how our own science can be enriched and how insightful hypotheses can be generated through the study of ethnobiology.

MATERIAL AND METHODS

Previous research by Posey (1981, 1983*e*, 1983*f*) was conducted in 1977–1979 during 14 months of field research with the Kayapó. During that period, data were collected while accompanying the Indians to the forest, savanna, and garden during annual ceremonial and seasonal cycles. Two bee "experts" served as principal cultural consultants, Kwyrà kà and his son Irã.

During the field period that resulted in this report (21 days during the months of August and September 1983), the original consultants were used and earlier materials were cross-checked by the oldest shaman of Gorotire, Beptopoop. Although Posey's previous fieldwork had met with few problems in acquiring data on bees, the presence of Camargo created unexpected complications. The Indians feared that his desire to collect bees would lead to the disturbance or destruction of their valued nests. Thus, it initially appeared that there had been a drastic drop in beekeeping, beekeepers, and bee nests in Gorotire since 1977–1979. However, this did not prove to be the case. In 1983, the Kayapó were simply distrustful of our curiosity about their stingless bees and reluctant to provide information or show us their nests.

Eventually, when we realized the source of complication, we were able to explain more specifically our intent and assure our hosts that their bee colonies would not be destroyed by our scientific efforts. Thereby, we were able to gain access to considerably more data, and receive more cooperative responses to our inquiries.

A "generative methodology" for eliciting was utilized; that is, formal questioning was held to an absolute minimum so as not to introduce our scientific paradigms into indigenous thought, thereby prejudicing responses.We simply communicated our interest in bees and let our consultants lead us to nests and tell us what they wished regarding bees and bee behavior. When questions were necessary, the most general formulations possible were utilized: for example, "Tell us about the bee's nest," or "Tell us about bee flight," and so on. The two major informants are fluent in Portuguese and routine conversation was carried out in that language. When consultants found difficulty in explaining any subject in Portuguese, communication shifted to Kayapó. New terms or concepts were recorded in the indigenous language and initial discussions of a new subject were carried out in Kayapó.

In addition to the collection of biological materials, drawings of bee nests were made in the field. Internal architecture was sketched and photographed if nests were opened by the Indians. Ethnographic notation occurred during all phases of the field study. Drawings in this article are based on information provided by Kayapó consultants. Fig. 1 is a replica of a drawing done in 1979 by Pedro Kayapó. Species encountered during this period of field research are listed in Table 1. Numbers preceding the species list refer to collection numbers in the Gorotire Kayapó collection now under the care of Prof. João M. F. Camargo and stored at the Departamento de Biologia, Universidade de São Paulo, Ribeirão Preto, São Paulo, Brazil.

RESULTS

Taxonomic Categories

Bees (social Apidae) are grouped along with other social insects as *nhy* (*ñy*), which is the only superordinate (supra generic) category found for Arthropoda (Posey, 1984*a*). Adults of social insect colonies are denominated *nhy*—thus ants are called *mrum-nhy,* bees are called *mehn-nhy,* wasps are called *amuh-nhy,* and termites are called *rorot-nhy. Apis mellifera* (*ngài-pere'y*) is often classified with wasps (*amuh-nhy*) rather than stingless bees (*mehn-nhy*) because of its powerful sting. On the other hand, wasps that produce honey (*Brachygaster* spp.) are often classified with bees rather than wasps because of their honey production.

Nests of social insects are given the same name as Kayapó houses, *ũrũkwa.* Likewise, traditional circular villages are said by the Kayapó

Table 1.—*Species of meliponine bees encountered in vicinity of Gorotire, Para, Brazil during the current study.*

Collection numbers	Scientific name	Kayapó name
(303c)	*Tetragona clavipes* (Fabricius)	ikài-kà
(304c)	*Partamona* cf. *cupira* Smith	myre-ti
(305c)	*Melipona seminigra pernigra* Moure & Kerr	udjy
(306c) & (308c)	[*Scaptotrigona nigrohirta* Moure Ms.]	imrê ñy kamrek
(307c)	*Scaptotrigona polystica* Moure	imrê-ti
(309c)	*Melipona melanoventer* Schwarz	menhirê ujdjà
(310c)	*Melipona rufiventris flavolineata* Friese	ngài kumrenx
(311c)	*Tetragonisca angustula angustula* (Latreille)	my krwàt
(312c)	*Tetragona dorsalis* cf. *beebei* Schwarz	tôtn my
(313c)	*Trigona fulviventris* Guérin	djô

to take the cross-sectional form of conical nests of wasps and bees (Posey, 1981).

*Nests of Meliponinae (*mehn nhy ũrũkwa*)*

External characteristics.—Nests of Meliponinae are grouped by the Indians according to external structures perceived as "natural discontinuities" or "natural" morphological groupings (Hunn, 1976). Although these groups are not linguistically labeled, their saliency as covert (unnamed) categories is easily demonstrated through field recognition and informant responses. Each nest-form group is typified by a "focal species" that has idealized qualities characterizing the set. Each set may be identified or referred to by the name of the focal species (as described in Posey, 1984*a*). Fig. 1 is a drawing produced by Pedro Kayapó, a young Indian man (*menononure*) from Gorotire, and illustrates the external form and internal structure of the focal species *kukrãi-ti* (*Trigona amazonensis*). Similar drawings by various Indians were used to construct the basic focal forms of the major nest categories summarized in Fig. 2. These focal forms are as follows: 2A, *kukrãi-ti* (*Trigona amazonensis*) constructs nests attached externally to large tree trunks or boulders; 2B, *me-nô-rà-kamrek* (*Trigona cilipes*) usually constructs nests in arboreal ant (*Azteca* spp.) colonies or termite (*Nasutitermus* sp.) nests; 2C, *mehñy-tyk* (*Trigona branneri*) prefers externally attached nests on various palm species; 2D, *imrê-ñy-kamrek* (*Scaptotrigona nigrohirta*) constructs nests in natural openings in tree trunks and builds entrance tubes of soft wax and resin (this is the largest category, encompassing a variety of genera and the species); 2E, *myre-ti* (*Partamona* cf. *cupira*) that builds in arboreal termite nests; 2F, *djô* (*Trigona fulviventris*) prefers subterranean nests, often found in termite

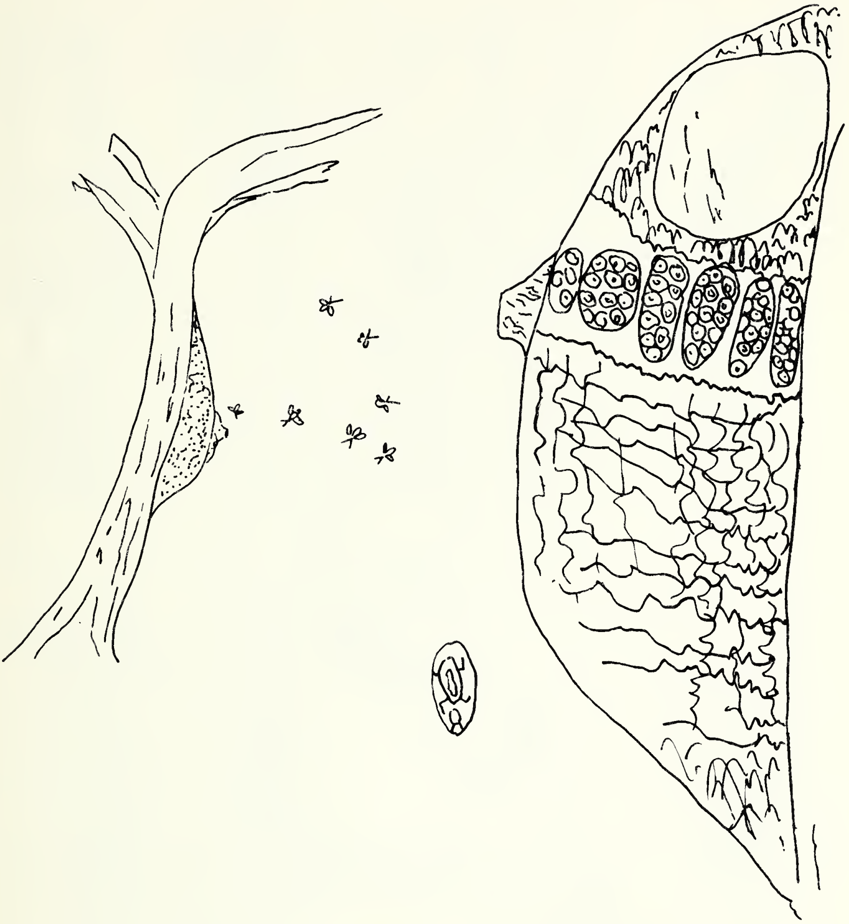

Fig. 1.—Reproduction of a drawing by Pedro Kayapó (made in Gorotire in 1979) showing the external form and internal structure of *ku-krãi-ti* (*T. amazonensis*).

nests; 2G, *puka-kam-mehn* (*Trigona recursa*) a subterranean nest-building species; 2H, *mykrwàt* (*Tegragonisca angustula*) usually found in hollow trunks of dead trees lying on the ground; 2I, *ngài kumrenx* (*Melipona rufiventris flavolineata*) found in open tree hollows, with an entrance tube hidden inside; 2J, *mehnô-djành* (*Frieseomelitta* sp.) found in hollow vines or bamboo.

A limited number of species is found in any given habitat. Certain species are habitat specific, that is, found only in savanna, or flood

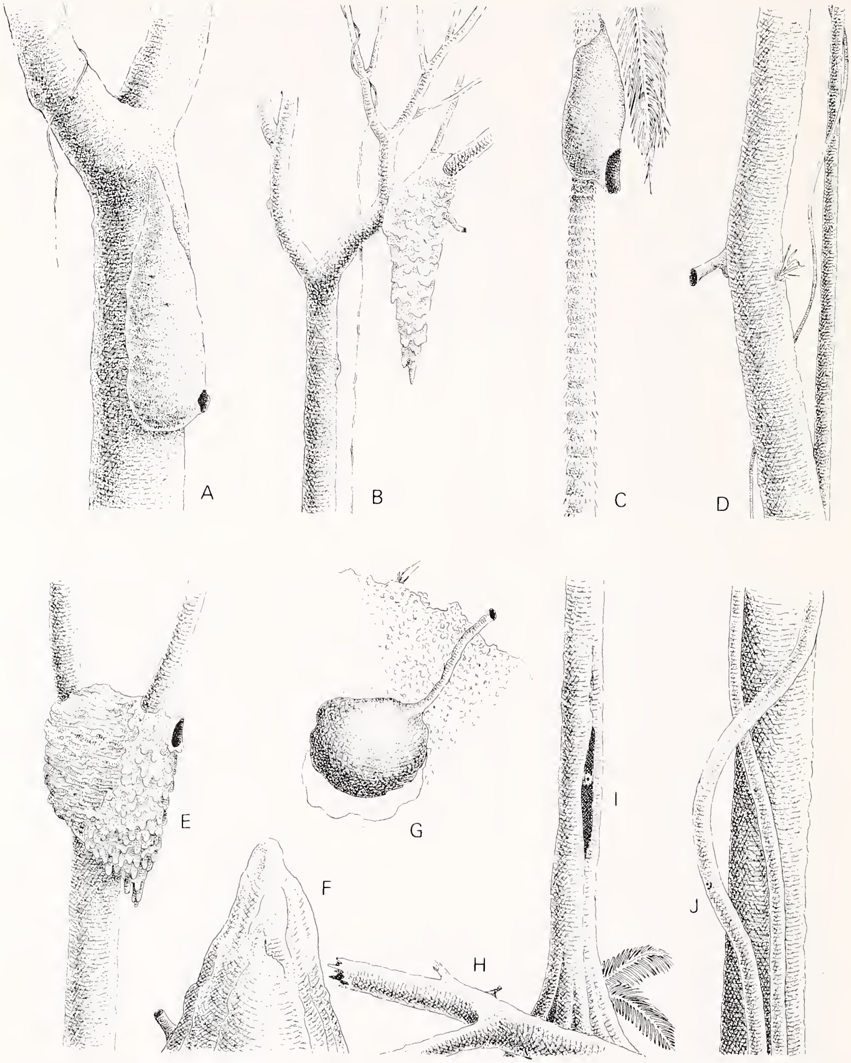

Fig. 2.—Nest types of Meliponinae focal species recognized by the Kayapó: (A) *Trigona amazonensis* (*ku-krãi-ti*); (B) *Trigona cilipes* (*me-nô-rà-kamrek*), inside termite nest; (C) *Trigona branneri* (*mehñy-tyk*); (D) *Scaptotrigona nigrohirta* (*imrê-ñy-kamrek*); (E) *Partamona* cf. *cupira* (*my-ti-re*), in termite nest; (F) *Trigona fulviventris* (*djô*); (G) *Trigona recursa* (*puka-kam-mehn*); (H) *Tetragonisca angustula* (*my-krwàt*); (I) *Melipona rufiventris flavolineata* (*ngài-kumrenx*); (J) *Frieseomelita* sp. (*mehn-nô-djành*).

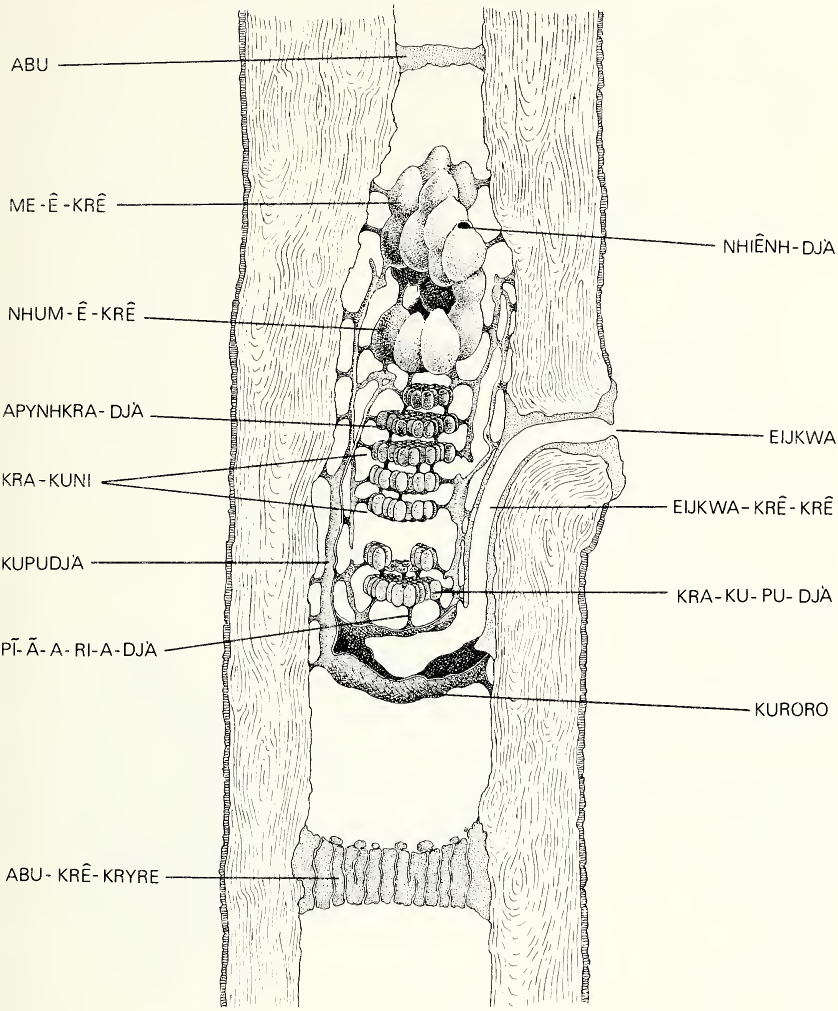

Fig. 3.—Schematic structures of *Melipona* nests with Kayapó nomenclature: *abu* (batumen), *me-ê-krê* (honey pot), *nhum-ê-krê* (pollen pot), *apynh kra-djâ* (brood cell), *kra kuni* (brood comb), *kupu-djà* (involucrum), *pĩ-ã-ari-a-djà* (pillar), *abu-krê-kryre* (lower batumen with drainage channels), *nhiênh-djà* (pot opening), *eijkwa* (entrance structure), *eijkwa-krê-krê* (entrance gallery), *kra-ku-pu-djà* (cocoon), *kuroro* (shell of nest).

forest, or high forest, and so forth. Thus when an Indian enters a specific habitat, he already knows, which species might be found, thereby facilitating visual scanning for morphological nest types.

Internal nest structure—Architecture and entrance structure.—Ter-

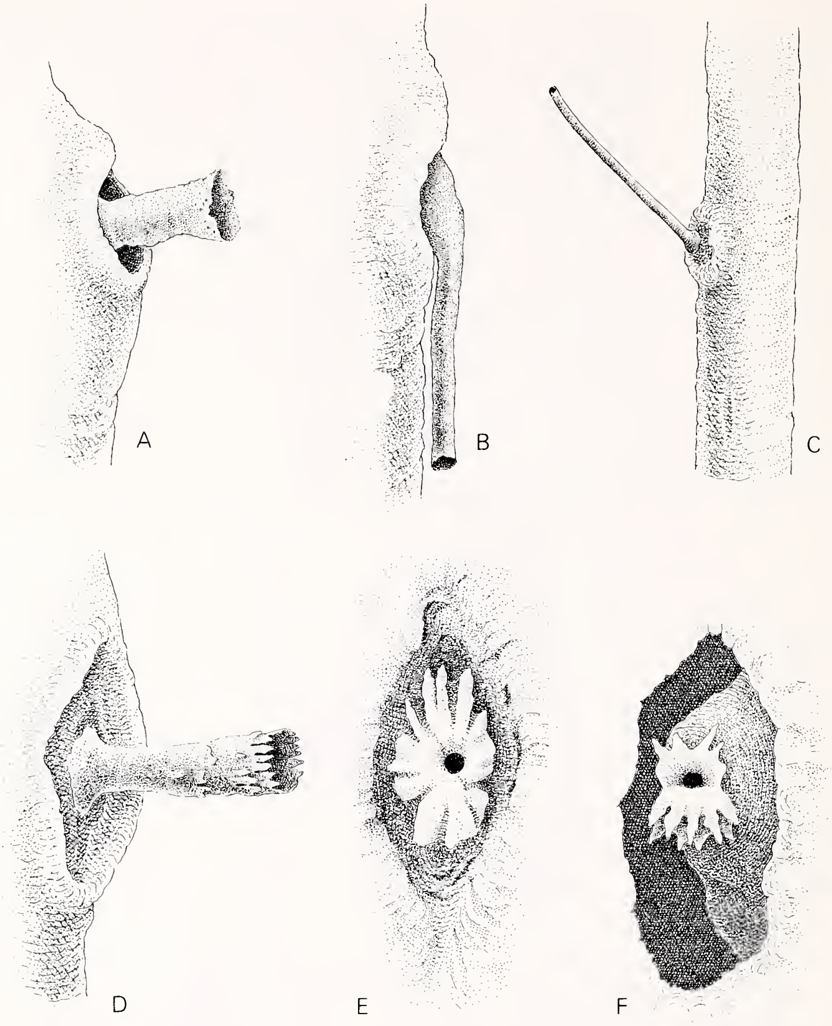

Fig. 4.—Types of Meliponinae entrance tubes recognized by the Kayapó with their respective "focal species": (A) *imrê-ñy-kamrek* (*Scaptotrigona nigrohirta*), (B) *imrê-ti* (*S. polystica*), (C) *õ-i* (*Tetragona truncata*), (D) *udjỳ* (*Melipona seminigra pernigra*), (E) *menhire-udjà* (*M. melanoventer*), (F) *ngài-kumrenx* (*M. rufiventris flavolineata*).

minology for structures of Meloponinae nests (*ũrũkwa*) is quite complete. Two types of nests, based on internal structure, are recognized by the Kayapó—nests with horizontal, parallel combs; and nests with dispersed caches of combs. The latter is represented in Fig. 1 and the former is reconstructed in Fig. 3.

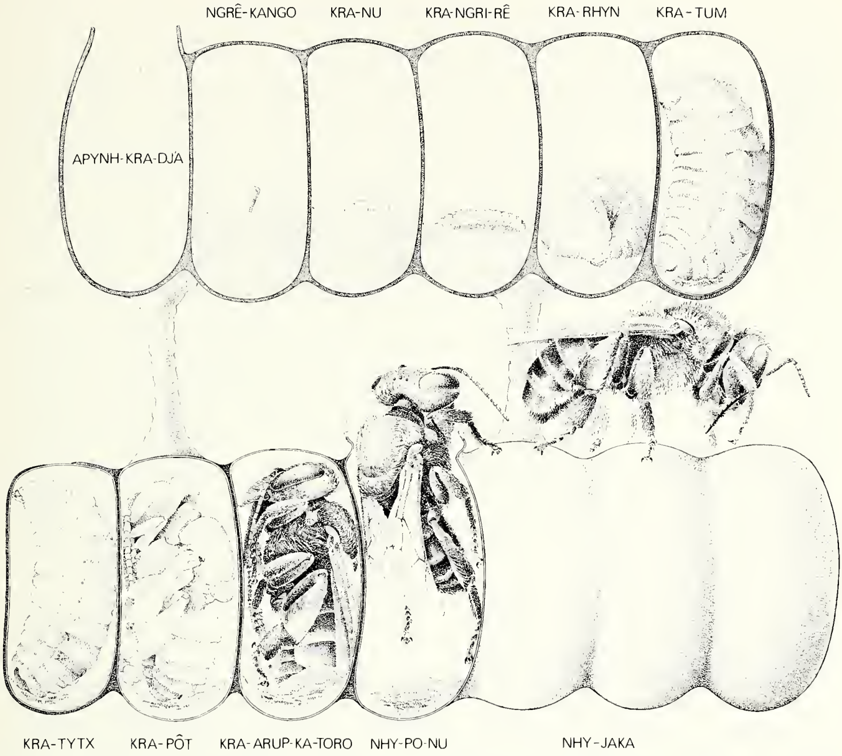

Fig. 5.—Ontogenetic stages of Meliponinae (represented in this figure by *Melipona compressipes fasciculata, ngài-re*) recognized by the Kayapó; *apynh-kra-djà* (brood cell); *ngrê-kango* (egg, egg liquid); *kra-nu* (larva of 1° instar); *kra-ngri-re* (larva of 2° instar); *kra-rhyn* (pre-defecant larva); *kra-tum* (post-defecant larva); *kra-tytx* (pre-pupa); *kra-pôt* (unpigmented pupa); *kra-arup-ka-toro* (pigmented pupa with movement); *nhy-pô-nu* (imago, emerging adult); *nhy-jaka* (newly emerged adult).

Fig. 3 shows the principal architectural structures with associated Kayapó names. A glossary of Kayapó terms and their English or scientific equivalents is found at the end of this article.

For the Indians, entrance structures (*eijkwa*) of meliponine nests are important diagnostic characters because each stingless bee species produces a specific structure. Shape, size, composition, color, position, and smell of the *eijkwa* are all characteristics used by the Indians for field identification. Fig. 4 shows the major *eijkwa* focal categories. These are covert categories, but as with nest forms, they are frequently identified by referring to the name of the focal species that typifies the category.

Onotogeny, Life Cycle, and Castes of Mehn-nhy *(Meliponinae)*

The Kayapó believe that bees, like Indians, have a life cycle associated with the social space of their villages (*kri-metx*) and houses (*ũrũkwa*). A bee's life begins in "a growing up thing" called *apynh-kra-djà* or "child sleeping place" (*kra-no-ro-djà*) (see Fig. 5). Combs are called *kra-ỳ-trỳ* and are filled with various stages of life, including the egg (*ngrê*). According to the Indians, however, bees do not have "true eggs" (*ngrê-kumrenx*) because they have no hard shell (*kà*). Instead, bee eggs are composed of a liquid deposited in the cell. This liquid is called *ngrê-kangô* (egg liquid) and becomes "new (bee) children," *kra-nu,* that in turn grow into "small children," *kra-ngri-re.* Subsequent stages of larval development are denominated by the Indians as follows: *kra-rhyn* ("round, thick children" that occupy the whole cell—known scientifically as predefecating larvae); and *kra-tum* ("old children" that stand up vertically in the cell—known scientifically as postdefecating larvae). When the shells (*kà*) of the "children" (*kra*) harden (*arup-tytx*), the bee child is thought to be fully grown and is called *kra-tytx* ("tough," or, in this context, "grown," "children"—scientifically known as prepupae). When the bee child takes on the appearance and size of an adult, it is called a *kra-pôt* ("grown child" that still cannot walk or move like an adult [*kra-pôt-ket-rã-ã*]). This is the primary pupae, just prior to eclosion. When the grown child begins to walk like an adult (*kra-arup-ka-toro*) after leaving its cell, the bee is known as *nhy-pô-nu.* Newly emerged adults are called *nhy jaka* (unpigmented or "white" bees) or *nhy rêrêk* ("weak bees"). As pigmentation begins to appear in the newly emerged adults, they are then called *nhy-ngri-re* ("small" or "callow" bees).

According to informants, adult bees have different activities and functions in the nest and are given different names. These types, based upon behavioral differences, are:

mehn akrê—"warrior bees" that defend the nest (aggressive bee species have more warriors than non-aggressive species).

mehn-ôkabin-djwynh—"scout bees" that search for food, water, or mud, as well as for new nest locations should the colony need to move or divide; these also help guard the nest and alert the "warriors" should there be any threat of danger.

mehn-ô-petx-djwynh—"worker bees" that collect pollen (*a-ũ*), nectar (*rã-kangô*), and resins (*kunõ*), as well as other materials necessary for the colony.

benadjwyrà-ratx—this is the "principal chief," who lives in the center of the comb. He is always larger than the rest and is said to eat differently than other bees (he eats pollen, *nhum,* and honey, *rã-*

kangô, whereas other bees eat only honey). He is responsible for coordinating and ordering all of the activities of the colony. In times of danger, he always hides in the interior of the nest at a safe distance from the brood comb. (The *benadjwyrà ratx* corresponds to the physogastric queen known to our science.)

benadjwyrà—these are the sub-chiefs whose duty it is to transmit the orders of the principal chief. Each of these (there may be several to many depending on the size of the nest) is in charge of a group of bees made up of individuals from each of the categories (or "castes"). (These correspond to virgin queens in bee biology literature.)

benadjwyrà-pron—these are the wives of the chiefs and are in charge of the egg-laying and care of children. These bees remain close to the combs and have a slightly enlarged abdomen, thereby giving the impression that they are larger than other worker bees. (Scientifically these are known as nurse bees.)

benadjwyrâ-nhõ-kra—these are the young children of the chiefs. They receive special food and always are found in the periphery of the comb. (These are queen larvae and pupae.)

Food and Feeding

*Pollen (*a-ũ*)*—The Indians say that pollen (*a-ũ*) is collected from selected flowers (depending on bee species' preferences) and carried to the nests (*ũrũkwa*) where it is stored in special pots (*nhum-ê*). To obtain the *a-ũ,* bees rotate their back legs (*mêtê*) near the flower, sometimes having previously put resin (*kunõ*) on their legs to assist in securing the pollen grains to the body (*tê'a-ma*). The process of obtaining and carrying pollen to the hive is called *mêtê kam ami tê o wai ri.* When the *a-ũ* actually reaches the hive, it is mixed with drops of water from the bee's mouth and stored in the *nhum-ê*; the pollen now receives another name, *nhum,* signifying its transformation by the water mixture. *Nhum* is the food for larvae (*kra*) in general; a special mixture with honey (*mehn-kangô*) is used to feed the chiefs and their children. Pollen of some species is eaten by the Kayapó (Posey, 1983*f*).

*Honey (*mehn-kangô*)*—*Mehn-kangô* is formed from nectar of flowers (*pidgô-rã-kangô,* or "flower water"). It is carried by the bees in their mouths to be stored in special pots, *mehn-ê-krê.* The Indians say that honeys from different flowers have different tastes and consistencies and must be mixed by the bees to produce a uniform honey (*mehn-kangô-aben-kôt*). Watery honey is said to be new honey, not yet properly mixed. When a proper mixture is completed, the honey is said to be "ready" or "already good" (*arup-metx*) and the openings to the honey pots (*nhiênh-djà*) are closed with cerumen (*ãn-jê*). Honey is the principal food of adult bees (*mehn-nhy*). Honeys of many species are valued as human food and as medicinals; some honeys are dangerous and can cause stomach ache and diarrhea (Posey, 1983*f*). Some bee species (for example, *i-kài-kà, T. clavipes*) are said to throw out their old honey at the end of the dry season to make room for the new honey of the wet season. This honey, or any honey that is considered old or acid (fermented), is called *mehn-kangô-kaigo* ("honey that serves for nothing").

Bee Morphology

Morphological structures of bees receive names that, for the most part, are analogous to parts of the human body. Some names, however, are used specifically for insect morphology. Fig. 6 shows most of the major morphological structures named by the Kayapó. Names were given in the field when Kayapó collaborators were shown live specimens. The glossary at the end of this article gives English and/or scientific equivalents to the Kayapó names.

Family Groupings and Specific Determinations

The superordinate (suprageneric) grouping of social insects (*nhy*) and various covert (unnamed) categories with focal species based on idealized nest and entrance structure morphology have already been discussed. Data to date are not yet complete enough to fully outline the Kayapó notion of relatedness between folk species of bees. However, several groupings made by the Indians (*õmbiqwa*) can be elaborated—for example, *imrê* (corresponding to the genus *Scaptotrigona*), *kangàrà* (corresponding to the genus *Oxytrigona*), and *ngài* (various genera related in a system as yet undescribed). Family groupings and specific determinations are based on the following characteristics.

Ethological characteristics.—(a) Flight patterns (how the bees fly when entering the nest); (b) degree of aggressive behavior when the nest is disturbed (aggressive to docile); (c) sound produced by bees in flight or by nocturnal behavior inside nest; (d) places bees visit, including types of flowers, dead animals, feces, sand banks, mud, and other sites.

Nest structure and habitat niche.—(a) Substrate preferred (for example, tree hollows, ant nests, termite mounds, inside earth, large trees; in the case of tree nests, nest form and position of the entrance structure is also important); (b) preferred habitat (flood forest, humid forest, savanna); (c) form, texture, color, and size of the entrance structure; (d) material utilized to construct the entrance structure (for example, mud, resin, cerumen, vegetable fibers, excrement); and (e) form and texture of the batumen (nest cavity boundaries or covering).

Morphological and biochemical characters.—(a) Shape of the bee's body; (b) colors of the bee; (c) designs or markings on body; (d) size and color of wings; (e) size of the bee; (f) smell of the bee (either its

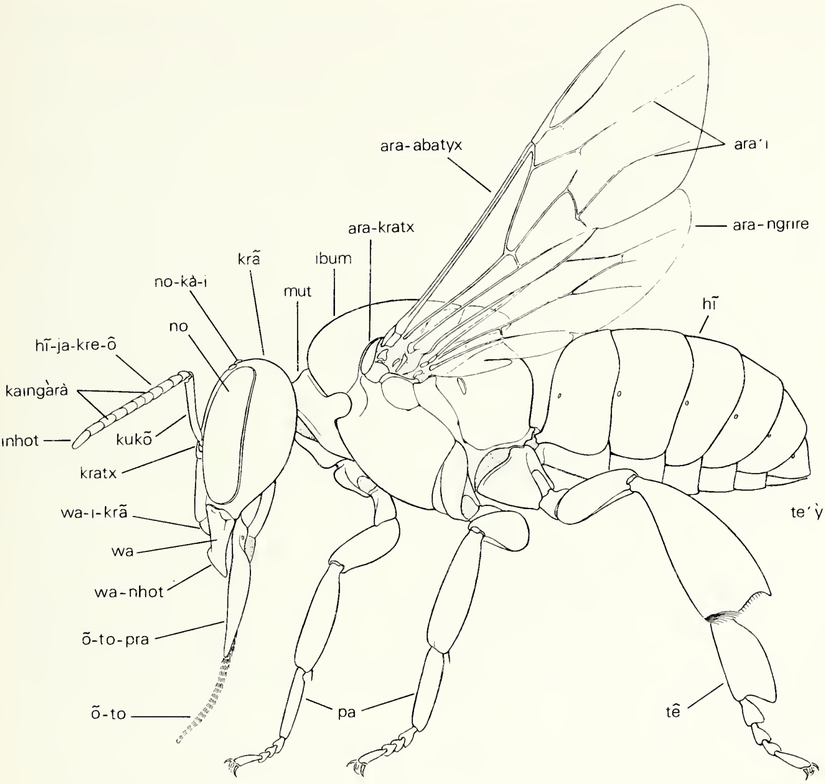

Fig. 6.—Major morphological structures recognized and named by the Kayapó: *ara-abatyx* (fore-wing), *ara-ngri-re* (small, hind wing), *ara'i* (veins), *ara-kratx* (wing joint), *krã* (head), *nô-kà-i* (simple eyes, ocelli), *nô* (compound eye), *hĩ-ja-krê-ô* (antenna), *kaingàrà* (segments of antenna), *inhot* (end point—distal), *kukõ* (base of antenna), *kratx* (joint), *wai-krã* (labrum), *wa* (mandible), *wa-nhot* (teeth of mandible), *õ-to-pra* (proboscus), *õ-to* (tongue), *mut* (prothorax), *ibum* (thorax/mesothorax), *pa* (front legs), *tê* (back legs), *hĩ* (abdomen), *tê'y* (point of abdomen).

naturally occurring smell or when the bee is crushed); (g) secretions produced for defense.

Economical factors.—(a) Quality of honey; (b) quantity of honey; (c) quality of resins; (d) quality of wax and cerumen; (e) suitability of pollen for food; (f) suitability of larvae/pupae for food.

Oxytrigona (*kangàrà*) are grouped into one family because of a liquid produced from glands in the mandibles for the purpose of protection. This liquid blisters and burns the human skin after a period of about 24 hrs, unless introduced subcutaneously, when blisters appear immediately. Texture and form of the nest entrance is also a unifying characteristic of this group, which makes long, slender slits slightly lined with cerumen, as in nest entrances. It is interesting to note, however, that *Partamona vicina* is named *kangàrà-kàk-ti* (the "big false *kangàrà*") because of its similar size and color with other *kangàrà*; it is also a very aggressive species, although it exudes no defense liquid. At the superordinate level, *Melipona* may only be grouped in covert categories, because no named groupings seem to unite the genus despite similarity in morphology. *Apis mellifera* is sometimes grouped with *Melipona* because of its size and color, although it is also frequently grouped with wasps (*amuh*) because of its sting. Other "functional" groupings include aggressiveness, as well as honey or cerumen types.

Arboreal nesting *Trigona* are always grouped together as *ku-krãi* (for example, *kukrãi-re, T. dallatorreana,* and *ku-krãi-ti, T. amazonensis*). *Scaptotrigona* (*imrê*) are grouped into the same family on the bases of similarity in honey, cerumen, and, principally, by their similar smells.

Summary of species collected.—The species described below were collected in Gorotire in 1983. They are presented with a summary of important diagnostic characteristics utilized by the Kayapó. (Note: these are some of the species most commonly mentioned by the Indians; other species can be found in Posey, 1983*g*:156). Order of characteristics is: (a) flight pattern when entering nest; (b) preferred habitat; (c) nest site; (d) smell of the bee; (e) form, texture, smell, and material utilized for entrance structure; (f) size and color of body and wings; (g) defense behavior.

Tetragona clavipes (*i-kài-kà,* "blade of knife")

a) smooth, circular flight before entering nest
b) forest where light penetrates (*bà-kamrek/bà-ràràrà*)
c) tree hollows (usually high up)
d) characteristic smell
e) large entrance tube of cerumen
f) yellow body, large wings, lightly colored
g) not aggressive (do not attack or bite); deposit resins

Observations: Throws out old honey at the end of the dry season to prepare for new, wet season honey.

Partamona cf. *cupira* (*my-ti,* "big penis")

a) rapid flight, direct entrance/exit pattern
b) savanna and forest
c) termite nests (*rorot, Nasutitermes*)
d) smell not distinctive
e) earth and resins

f) black body, white wings
g) very aggressive (bites and attacks)

Observations: Quantity of honey small, but very important for medicine.

Melipona seminigra pernigra (*udjỳ,* "witchcraft")

a) no information (not discussed by the Indians)
b) high forest (*bà-tyk*)
c) hollows of big trees
d) no information
e) entrance tube long, made of mud and resins
f) big bee with black thorax (*ibum-tyk*)
g) not aggressive

Observations: This is a "semi-domesticated" species that returns to the nest when a portion of the brood comb with honey and pollen pots are left in the old hive; this bee is also kept near the house simply to observe as a curiosity; honey is good year-round; bees are used in witchcraft.

Trigona amazonensis (*ku-krãi-ti,* "like a mountain ridge")

a) no information
b) high forest and mountains (*krãi*)
c) attached externally to tall trees and large rocks
d) no information
e) large lower structure made of same material as nest cover
f) large black body, clear wings
g) very aggressive (attacks and bites)

Observations: Honey of large quantity and good taste, taken mostly in the dry season; bees are crushed and mixed with *urucú* (*py*) to paint dogs so they will be aggressive (*akrê*) and have no fear of hunting. Fire, smoke, and *kangàrà-kanê* (see following section) used to extract honey and wax. Honey pots are placed over banana leaves and mashed to release honey. Larvae and pupae are crushed and rubbed on hunting dogs to make them strong (*tytx*).

Scaptotrigona nigrohirta (*imrê-nhy-kamrek,* "red imrê"—a Kayapó proper name)

a) no information
b) várzea forest (*imô*) and light-penetrating forest
c) hollows of medium to large trees
d) distinctive smell
e) tube of yellow cerumen when new; turns dark when old

f) yellow body, white wings
g) very aggressive (attacks and bites); attacks other bees by biting their wings

Observations: Honey good all year; combs with larvae are utilized for food and said to taste like "cookies;" pollen also eaten, but only if yellow, which indicates it is sweet; it is believed that this bee has more than one principal chief (*benadjwyrà-ratx*); cerumen is used to make the ceremonial hat, *mẽ-kutôm.*Method of bee's aggressiveness, attacking others by breaking their wings, may be related to Kayapó idea of *aben-tak* (traditional ceremonial sword fight aimed at breaking long bones of arm); only descendants of chiefs said to receive the proper name of *imrê.*

Scaptotrigona polystica (*imrê-ti,* "big *imrê*"—a family of bees and Kayapó ceremonial name)

a) no information
b) várzea forest (*imô*)
c) hollows of medium to large trees
d) characteristic smell
e) long, tough black entrance tube, pointed downward next to the trunk
f) black body, clear wings
g) not aggressive (*wajabôre*)

Observations: Large amounts of honey taken in dry season; lesser amounts of honey taken in wet season; cerumen used to attach feathers and coat cotton thread, as well as to make *mẽ-kutôm*; for other qualities, see *imrê-nhy-kamrek.*

Melipona melanoventer (*menire-udjà,* "vagina")

a) no information
b) várzea forest (*imô*)
c) hollows of medium to large trees
d) no information
e) shaped like a vagina; made of earth and clay; opening for one bee only
f) thorax (*ibum*) yellow
g) not aggressive

Observations: Produce a very distinctive noise at night that helps to locate and identify the bee; both honey and pollen are eaten; one of the "semi-domesticated" species.

Melipona rufiventris flavolineata (*ngài-kumrenx,* "true *ngài,*" a family of bees)

a) direct flight when entering
b) light-penetrating forest (*bà-ràràrà/bà-kamrek*)
c) tree hollows close to the ground (always less than one meter), frequently in dead tree trunks
d) strong smell; easily detectable when colony is swarming (*abem-o-watõ*); odor trail of swarm followed by Indians to locate new bee colony
e) mud (*ngỳ*) and bark fibers (*piã-õm*); hidden inside tree hollow
f) yellow body
g) not aggressive

Observations: Honey very sweet and taken all year; "semi-domesticated" in village and old gardens (*puru-tum, ibê-tum*); distinctive sound at night used to locate hive; bees followed from sides of rivers and igrapés when collecting water, mud, and other materials.

Tetragona dorsalis (*tôtn mỳre,* "penis of armadillo")

a) circular, smooth flight before backing off to enter in a direct flight
b) high forest (*bà-tyk*)
c) hollows of trees
d) distinct smell from resins carried by bees
e) small entrance tube of resin; strong smell from resin; shaped like penis of armadillo
f) yellow body, white wings
g) not aggressive

Observations: Honey good all year; bees produce distinct noise when swarming; odor trails of swarm followed by Indians to locate new nest; when new nest is located, Indians wait five to ten years before opening to take honey; division of nest by bees occurs only in wet season; smoke from strong-smelling resins (collected by bees) used to purify houses and body to expel spirits and sickness; resins burned as incense; cerumen and batumen also burned and smoke inhaled to cure "dizziness" or "craziness" (*eijbam*). Nest located in forest by listening for call of a bird (*tô-wa-pê-tê, Hypocnemis* cf. *candator*) known to prey upon adult bees near nests.

Tetragonisca angustula angustula (*my-krwàt,* "ridged long penis")

a) slow flight, circles, then retreats before entering in direct flight pattern
b) wide-spread, prefers light-penetrating forest
c) hollows of dead trees lying on ground
d) no information
e) thin tube of yellow cerumen

f) small, yellow
g) not aggressive (*wajabore*)

Observations: Honey highly appreciated and taken all year; larvae and pollen eaten; sound of colony at night not loud, but distinctive; bees caught in rain hide under leaves for protection; if they cannot return to hive at night they die; worker bees fly in straight lines from resources to nest and can be followed to find nest; "semi-domesticated" near houses and old gardens; resin used to attach arrow points.

Trigona fulviventris (*djô,* significance of name unknown)

a) no information
b) margin of forest (*bà-kôt*) and savanna (*kapôt*)
c) subterranean, often in termite nests (*rorot*)
d) no information
e) black tube with pieces of bark fiber
f) black
g) not aggressive

Observations: Honey taken all year, but of small amount; wax used for artifacts and to produce medicinal smoke.

Collection, Exploitation, and Social Significance of Meliponinae

Honey, cerumen, and other products associated with Meliponinae are important economic elements in Kayapó society (Posey, 1983*e,* 1983*f*). One of the principal reasons men give for going to hunt is to procure honey.

Bee specialists in Gorotire are all shamans (*wayanga*), which is not surprising because it was the ancient shamans who conceived of the "natural model" for Kayapó social organization based upon social Hymenoptera studies (Posey, 1981, 1983*d*). One of the shamans' secrets of finding bees is to walk at night listening for the distinctive sounds of colonies ventilating their nests. Most Indians are afraid to leave the village at night for fear of spirits (*karon*); shamans, however, do not fear *karon.* They mentally mark, spacially and temporally, the nests heard at night, then return in the day to observe the colonies. Of the colonies described in this paper (see preceding section), seven were located during night hunting trips. Indians also locate nests by observing flight patterns of bees returning from collection visits at river and stream margins. Indians have been observed (by Posey) running quickly behind a bee to locate its colony. Trails of odor (*mehn-nhy-pry*) of bee swarms are followed as though they were trails of game, such as wild pig or tapir. Bees are believed to always fly upwind toward their nest when leaving a food or water source. An Indian may observe for hours the flight patterns and activities of bees near flowers or margins of water.

Presence of a bee's nest, once found by a Kayapó individual, is generally announced in some public place (the men's house, *ngà,* or river landing, *ngô kà*) so as to advise others of its discovery and intent by the finder to exploit the colony at some future time. This is done by describing the nest's habitat and geographical location, as well as identifying the bee itself. The finder then has usufruct rights to the colony. If another person raids the claimed colony, misunderstanding and anger can result. Tirades against poachers are sometimes heard in the men's house. Usufruct claims are strongest when bee colonies are located in the old gardens (*puru-tum* and *ibê-tum*) of the finder.

A variety of technologies is used to exploit colonies depending on the nest site, habitat, and aggressiveness of the species. Nests of non-aggressive species (*wajabôre*) are simply opened with axes when the tree is not too large nor the nest too high. With large trees or extremely high nests, the Indians build a special platform with ladders to get to the colony. This platform can be quite elaborate, with several stages, all carefully constructed from poles tied together with vines. In large trees or trees of very hard wood, holes are opened only large enough to insert the hand and arm to pull out the brood and honey pots. Nests high in trees of less than one meter circumference are taken by cutting down the tree. The opening in the forest produced by the fallen tree (*bà-krê-ti*) is later utilized for planting medicinal and food plants (see Posey, 1983*a,* 1983*b,* 1984*b*). These forest openings also attract game and birds for hunting. Thus exploitation of bees figures prominently into the overall system of forest management practiced by the Kayapó and leads to the diversification of floral and faunal species that occur in the forest (Posey, 1984*b*).

Aggressive bees (*akrê,* such as *T. amazonensis, Oxytrigona tataira,* and *Apis mellifera,* are taken with fire and smoke. Dry leaves of palms and wild banana are attached to long limbs and are set on fire. The burning, smoking mass is held near the entrance of the nest to expel the bees. Sometimes trees are then felled and fires built near the opening of the nest.

Another effective method of expelling aggressive bees is to put the shaving of a highly toxic vine called *kangàrà-kanê* (*Tanaecium nocturnum*) into the nest opening (Kerr and Posey, 1985). In a short time (1 to 4 min) the volatile components of the vine stun or kill enough bees so that the nest can be safely opened. Leaves of the same plant are chewed and the saliva–plant mixture passed over the body to prevent stings or bites from the bees. Although we were unable to confirm this, the Indians state that the use of *kangàrà-kanê* is only to stun the bees, not to kill the colony; thus it is left in the colony for only a short time.

We had the opportunity to observe the use of *kangàrà-kanê* by *Kwyrà-kà* with *M. rufiventris flavolineata.* After a small ball (10 cm diameter) of the shaving was put into the opened nest, bees began to die in only 1½ min. Within 4 min the entire colony was dispersed or dead.

Nests of some species, including *M. seminigra pernigra, M. melanoventer, M. rufiventris flavolineata, Scaptotrigona nigrohirta,* and *S. polysticta,* are exploited year after year in the fields and forests. This is possible because after opening the colonies and taking a portion of its contents, parts of the brood comb, honey, pollen, and cerumen are returned to the nest. The Kayapó say this is to keep *Bepkôrôrôti* happy. *Bepkôrôrôti* is the spirit of an ancient shaman who becomes angry if food is not shared (he has a particular penchant for honey) and will send lightning and thunder to destroy those who are greedy (see Posey, 1983*f*:65). Thus, *Bepkôrôrôti* not only functions to encourage sharing in the tribe, but he also becomes the protector of bees and insures the preservation of bee colonies.

Nests of other species, for example, *T. angustula, T. dallatorreana,* and *T. cilipes,* are taken to the village in their natural substrates or put into special baskets called *kangri* (made of banana and wild banana leaves). We observed one colony of *T. angustula* being carried to the house of *Kwyrà-kà* in a *kangri* to be "kept" (*õ-krit*) in a cool, dark place in his house in Gorotire. "Semi-domesticated" bees that form the list of *õ-krit* species are found in Table 2.

General Observations and Notes

The Indians recognize many ecological relationships between bees and other ecosystem components. Plants that produce flowers that attract bees are left to grow, or are even planted, in gardens and alongside forest trails. The Kayapó say that when there are many bees, there are abundant crops. The relationship between bees and crop production, as well as the folk concept of pollination, is yet to be studied in detail.

Relationships of bees with other animals are also recognized. For example, *T. chanchamayonensis* is known to frequently nest with an ant called *mrum-gogo* (still unidentified); *T. cilipes* likes to nest with another ant called *mrum-kudjà* (*Azteca* sp.). Certain bees are also frequently found cohabiting in the same tree or nest site, including *S. polystica, T. clavipes, S. nigrohirta, S. favisetis,* and *T. truncata.* Other bee species are always found alone, such as *M. compressipes fasciculata, M. rufiventris flavolineata*; *T. angustula, M. seminigra pernigra,* and

Table 2.—*Bee species semi-domesticated by the Kayapó Indians.*

Kayapó name	Scientific name
imrê-ti	*Scaptotrigona polystica* (Moure)
imrê-ñy-kamrek	*Scaptotrigona nigrohirta* Moure Ms.
ku-krãi-re	*Trigona dallatorreana* (Friese)
mehnô-rã-kamrek	*Trigona cilipes pellucida* (Ckll.)
mehnô-rã-tyk	*Scaura longula* (Lep.)
menhire-ujdà	*Melipona melanoventer* Schwarz
*my-krwàt	*Tetragonisca angustula angustula* Latreille
ngài-kumrenx	*Melipona rufiventris flavolineata* Friese
ngài-pêrê'ỳ	*Apis mellifera* Linn.
ngài re	*Melipona compressipes* cf. *fasciculata* (Smith)
*udjy	*Melipona seminigra pernigra* Moure and Kerr

* These names represent revision (corrections) in names used in previous publications (that is, Posey, 1983*e*: Table 3; and Posey, 1983*f*: Table 2).

M. melanoventer. Two wasps are known to be predators of bees; these are *amuh-kamrô-tyk* and *kukryt-anhoroti* (identifications not yet made). Certain bees of the *imrê* family (*Lestrimelitta limão* Prov.) are known by the Indians to rob honey, pollen, and other nest materials from other colonies. Some species of *Scaptotrigona* are likewise known to pillage nests of other bees. A bumblebee, *kungont* (*Bombus transversalis*), is famous as a robber of pollen (Weaver, 1978). The mammal called *krok-krok-ti* (*irarâ, Eira barbara*) is despised because it destroys the nests of the semi-domesticated species when searching for its favorite food, honey. The small bird *tõ-wa-pêtê* (*Hypocmenis* cf. *cantator*) helps the Indians locate bee hives because it sings when successful in its attack on adult bees.

Another interesting phenomenon observed by the Indians is the coexistence of commensal acarines inside the bee colonies. These acarines are called *nhure* and are believed to be the property of the bees—each bee has its own *nhure* that it raises (*õ-krit*) just as Indians raise dogs. The *nhure* are said to eat the trash left by the bees (*mehnõ-ja'um*) just as village dogs clean up after the Indians.

In relation to the Africanized honey bee (*Apis mellifera,* generally known as the "Brazilian bee"), the Kayapó are keenly aware of its presence and effect in the region. They say that this bee (*ngài-pêrê'y*) arrived during the full moon in February 1966. The Indians report that this bee began to attack and pillage (*ỳr-wai-djà*) the nests of Meliponinae. Likewise, the *ngài-pêrê-y* are so aggressive as to attack other bees at flowers, particularly the flowers of *inajâ* (*Maximiliana regia*), as well as at water sources near the margins of rivers and streams. Bees that are particularly vulnerable to *Apis mellifera* are *imrê-ti* (*S. polys-*

tica), *imrê-nhy-kamrek* (*S. nigrohirta*), *udjy* (*M. seminigra pernigra*), *tôtn-my* (*T. dorsalis*), *my-krwàt* (*T. angustula*), among others. Currently the aggressiveness of the *ngài-pêrê-y* is said to have diminished, thereby allowing the native bees to peacefully gather pollen and nectar and therefore to produce more honey. The Kayapó do not like the *Apis* honey as well as that of the Meliponinae. *Apis* honey is usually traded or sold, whereas meliponine honey is kept for local consumption.

DISCUSSION

The purpose of this study is not to compare indigenous knowledge of Meliponinae with that of Western science, but to report indigenous knowledge to aid our search for new ideas about stingless bees and bee behavior. To this end, we feel our work, although only in its beginning phases in relationship to the complexity and sophistication of Kayapó knowledge, has helped to define some important and interesting areas for further biological research.

Characteristics used in Kayapó meliponine taxonomy are indeed similar to that of Western science, although the reliance upon chemical qualities (odors) of species needs to be further investigated. Likewise, bee behavioral groups recognized by the Indians (*mehn-akrê, mehn-ôkabin-djwynh, mehn-ô-petx-djwynh*) could represent actual divisions of labor in addition to those currently accounted for by age variations (see Kerr and Neto, 1953; Hebling et al., 1964; Bassindale, 1955; Sakagami, 1982; Wille, 1983).

Research to date documents communication by odor trails only for Trigonini, whereas in *Melipona* sound is thought to be the principal means of communication (Lindauer and Kerr, 1960; Lindauer, 1967; Esch et al., 1965; Kerr and Fales, 1981; Kerr, 1960; Kerr et al., 1963). The Kayapó, however, insist that other bees have trails of odor as well, including *M. rufiventris flavolineata,* which has an especially distinctive odor during swarming. Is there a chemical component in communication and orientation of *Melipona*?

Acarine mites that live with Meliponinae are little studied until now (Flechtmann and Camargo, 1974; Rosa and Flechtmann, 1983; Delfinado-Baker et al., 1983) and are considered commensal. The Indians, however, believe the species to be symbiotic. Can Indian knowledge give insights into this little-known subject?

Ecological zones and microzones preferred by specific species of Meliponinae is one of the specialities of the Kayapó, but these have not been systematically studied. However, factors affecting the tendency of certain species to share or not share habitats, as observed by the Indians, is of significance to ecological research (Roubik, 1979*a,* 1979*b*, 1983).

Impact of the invasion of the Africanized *Apis mellifera* into new ecological zones is also little known (Roubik, 1979*b,* 1980, 1981, 1983), yet it has been carefully observed by the Kayapó and deserves further study.

Another important subject that must be considered in future research is to what extent the Kayapó knowledge of biology is reflected in their social and cultural systems. Are their beliefs about social bee behavior (including social division of labor, moving of colonies, aggressiveness and attacks, pillaging, defense, differential food distribution, and other behavior) really only anthropomorphic explications of observed biological phenomena? Or, as the Kayapó insist, were these social and cultural patterns really intentionally developed based upon ideas and knowledge by an ancient shaman of social insect behavior? Was Kayapó society created upon an intentional "natural model" or is it simply explained by a "natural reality?" These are questions rarely raised by anthropologists or biologists, but should no longer be avoided.

Concluding Remarks

This and other published works on Kayapó knowledge of meliponines represent still only superficial treatment of a much larger and more complex body of indigenous information about stingless bees. Further investigation of this knowledge will have to proceed with care and perseverance to "discover" the more intricate aspects of Kayapó folk science. Frequently the most interesting and revealing cognitive structures and their logical constructions lie submerged in the nonverbal realm of indigenous thought. The noted bee expert of the Gorotire-Kayapó, Kwyrà kà, for example, was able to quickly and accurately separate for us numerous closely related *Trigona* species, but was unable to verbalize the reasons for such decisions. This is because his knowledge of nature comes from silently observing, rather than verbally analyzing. Observations are registered in a gestalt manner along with a myriad of information regarding niche, habitat, ecological zone, geographic coordinates, and associated elements of the same ecosystem.

Non-literate societies depend upon symbols transmitted orally for the dissemination of knowledge. Myth, therefore, functions as a compact vehicle for the transmission of ecological concepts (Posey 1983*b*). To understand myth and what it really communicates to the people who understand its symbols, the scientist must understand the symbolic language that generates and interprets the secrets of oral tradition. Until this is done, the ethnobiologist can never evaluate the validity of indigenous ideas about nature. Judgements of ideas as being "absurd," "impossible," "mere superstition," or just "quaint, with no true scientific value," must be purged from the self-proclaimed superiority of ethnocentric western science. In the true spirit of scientific inquiry, however, hypotheses can be generated, stimulated by indigenous ideas, and subsequently tested with proper scientific rigor. In this manner, ethnobiological research offers an unequalled philosophy and methodology for the enrichment and advancement of a world science.

One of the most valuable results of the investigation of Kayapó knowledge of meliponines is the understanding of how stingless bees are seen by the Indians as an integral part of a complex natural system. Clearings produced by trees felled to take honey, for example, serve as garden openings where medicinal and edible plants are planted and transplanted. Fruit trees and leafy vegetation also provide food for wildlife, with some species actually planted by the Indians to attract desirable game animals (Posey 1985). Thus management of bees is part of an overall strategy for the conservation and exploitation of secondary forest.

It is precisely this type of integrated knowledge, based upon intricacies of indigenous science, that offers many new ideas for those persons and institutions interested in long-term, ecologically and socially sound plans for development and conservation in the humid tropics (Parker et al., 1983; Posey et al., 1984). Thus specific studies such as this one on Kayapó knowledge of meliponines represent only initial stages of a truly comprehensive model of ethnobiological research. It is our hope that these notes will help to stimulate other ethnobiological studies that will, in turn, expedite the creation of the larger model, founded upon respect for other scientific systems and the urgency of their systematic study.

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GLOSSARY

English meaning of Kayapó Indian words.

Kayapó	*English*
abem-o-watõ	bee swarm
abu	batumen
abu-krê-kryre	lower batumen (with drainage channels)
akrê	aggressive
ãn-jê	close cell with wax
apynh-kra-djà	cell
ara-abatyx	large wing
ara'i	wing vein
ara-kratx	wing joint
ara ngri-re	small wing
arup-metx	good/ready honey
arup-tytx	already hard (pupae)
a-ũ	pollen
bà-kamrek	open forest
bà-kôt	forest margin
bà-krè ti	forest opening
bà-ràràrà	closed forest
bà-tyk	high forest
benadjwyrà	chief
benadjwyrà-nhõ-kra	chief's child
benadjwyrà-pron	chief's wife
benadjwyrà-ratx	principal chief
eijkwa	mouth/entrance
eijkwa-krê-krê	entrance gallery
hĩ	abdomen
hĩ-ja-krê-ô	antenna
ibê-tum	old field
ibum	thorax
imô	varzca forest
inhot	distal
kà	shell
kaingàrà	segments
kangàrà-kanê	"bee medicine"; medicinal vine
kangri	bee basket
kapôt	savanna
krã	head
kra-arup-ka-toro	pigmented pupae
kra-kuni	brood comb
kra-ku-pu-djà	cocoon

kra-ngri-re	2nd instar larvae
kra-no-ro-djà	brood chamber
kra-nu	1st instar larvae
kra-pôt	unpigmented pupae
kra-pôt ket rã'ã	still pupae
kra-rhyn	pre-defecating larvae
kra-tum	post-defecating larvae
kratx	joint
kra-tytx	prepupae
kra-ỳ-trỳ	comb
kri-metx	village
kukõ	base of antenna
kunõ	resin
kupu-djà	involucrum
kuroro	shell of nest
me-ê-krê	honey pot
mehn-akrê	warrior bees
mehn-ê-krê	honey storage pot
mehn-kangô-kaigo	fermented/spoiled honey
mehn-nhy-pry	bee odor trail
mehnõ-ja'um	bee trash
mehn-ô-kabin-djwynh	scout bee
mehn-ô-petx-djwynh	worker bee
mẽ-kutôm	beeswax hat
mêtê	rotate leg
mêtê kam ami tê o wai ri	put resin on leg to carry pollen
mut	prothorax
ngà	warrior's house
ngrê	egg
ngrê-kango	egg liquid
ngỳ	mud
nhiênh-djà	opening to pot; pot opening
nhum	stored pollen
nhum-ê	pollen pot
nhum-ê-krê	empty pollen pot
nhy (ñy)	social insects
nhy-jaka	newly emerged adult
nhy-ngrire	small adult
nhy-pônu	emerging adult
nhy-rêrêk	young, weak adult
no	eye (compound)
no-kà-i	ocelli (simple eye)
õ-krit	animal being raised
õ-to	tongue
õ-to-pra	tongue cover
pa	arm
pĩ-ã-ari-a-djà	pillar
piã-õm	plant fiber
pidjo-rã-kangô	nectar
pĩ-tum	dead trunk
py	anchiote, urucu
rã-kangô	nectar
ry	long, thin
tê	foot

tê'a-ma	affix pollen to leg
te'ỳ	end of abdomen
ũrũkwa	house
wa	mandible
wai-krã	labrium (labrum)
wajabore	non-aggressive
wa-nhot	teeth of mandible
wayanga	shaman
ỳr-wai-djà	invasion

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PELVIC MYOLOGY OF THE KINGBIRDS AND THEIR ALLIES (AVES: TYRANNIDAE)

MARY C. MCKITRICK[1,2]

ABSTRACT

The hindlimb muscles were studied in 43 species of tyrant flycatchers (Tyrannidae), of which 26 are in the monophyletic kingbird group. Series of up to 15 individuals of certain species were dissected. The study (1) provides the first comprehensive descriptions of hindlimb myology for New World suboscines; (2) tests Raikow's (1982) hypotheses about several passeriform synapomorphies; (3) examines the assumption that intraspecific variation in hindlimb muscles is sufficiently low as to have no impact on phylogenetic studies, and (4) assesses the value of the hindlimb musculature as a source of data for generating phylogenetic hypotheses for the Tyrannidae, particularly the kingbirds. Raikow's (1982) myological synapomorphies are confirmed for the Tyrannidae, but the assumption that individual variation is low is rejected for this group. The results show remarkable uniformity for most muscles within and among species, but the patterns of variation in several flexors are irregular and suggestive of multiple origin and loss within tyrannids, as well as atavistic reappearance in some cases. This may be atypical among birds, and dissection of even larger series of individuals would help to elucidate this issue.

INTRODUCTION

The present research was undertaken for four reasons. The most general of these was to address the need for comprehensive descriptions

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of the appendicular myology of a large group of suboscine birds, the New World flycatchers (Tyrannidae). George and Berger (1966:229) noted a great need for studies of the appendicular muscles in diverse groups of birds, in order to discover patterns of intergeneric variation. This need is particularly great for the New World suboscines. Apart from Hudson's (1937) study of the pelvic myology of a large number of birds, which included *Tyrannus tyrannus,* and the occasional references to *Procnias nudicollis* (Cotingidae) in George and Berger (1966), there are no published accounts of the limb muscles of this large and diverse group. Raikow (1982) made reference to dissections of a few species from several New World suboscine families, but published no descriptions. The present study provides the first complete, illustrated descriptions of the comparative hindlimb myology of any New World suboscines. It is intended to complement the work by McKitrick (1985*b*) on the pectoral myology of the kingbirds.

Second, this study tests Raikow's (1982) myological diagnosis of the order Passeriformes. Raikow presented several character states from the hindlimb musculature as probable synapomorphies for the passerines; these include the division of M. pubo-ischio-femoralis into cranial and caudal bellies, and the loss of most of the intrinsic muscles of the pes except for Mm. extensor hallucis longus, flexor hallucis brevis, and abductor digiti IV. His dissections of representative suboscine species support these hypotheses of synapomorphy, but further corroboration is needed from study of additional species.

Third, the present work attempts to test the assumption, traditional to studies of avian myology, that variation within species is sufficiently low as to have little impact on phylogenetic studies. The unavailability of large samples in museum collections has made such a test difficult until recently, when new awareness of the importance of this kind of material has encouraged the growth of collections of spirit specimens (Wood et al., 1982; see Raikow, 1985). The results of dissecting series of individuals of certain tyrannid species are presented herein. This analysis leads to the final reason for undertaking the present study, which is to determine whether the hindlimb musculature can provide useful information for studying phylogenetic relationships within the Tyrannidae, in particular the kingbirds. Relationships among and within the families of the New World Tyrannoidea (Tyrannidae, Pipridae, Cotingidae, Oxyruncidae, and Phytotomidae) have puzzled ornithologists for over a century (Snow, 1982), due possibly to the multiple origin of apparent similarities within the group. I examine the hindlimb muscles of the Tyrannidae in an effort to discover synapomorphies of use in phylogenetic hypotheses. For purposes of this study, I accept the hypothesis that the family is monophyletic on the basis of cladistic analysis of anatomical characters (McKitrick, 1985*a*), and further, that the kingbird group sensu Traylor (1977) is a clade (Lanyon, 1984). The kingbird group comprises 33 species in nine genera: *Pitangus, Megarynchus, Myiozetetes, Conopias, Myiodynastes, Legatus, Empidonomus, Tyrannopsis,* and *Tyrannus*; I concentrate my analysis on this group.

METHODS

The following 26 species from the kingbird group were dissected (sample sizes are given in parentheses when greater than 1): *Pitangus lictor, P. sulphuratus* (7), *Megarynchus pitangua* (2), *Myiozetetes luteiventris, M. cayanensis* (4), *M. similis* (15), *M. granadensis, Conopias inornatus, C. parva, C. trivirgata* (2), *Myiodynastes luteiventris* (4), *M. bairdii* (2), *M. maculatus* (5), *Legatus leucophaius, Empidonomus varius* (3), *E. aurantioatrocristatus, Tyrannus niveigularis, T. melancholicus* (7), *T. vociferans* (2), *T. crassirostris, T. verticalis* (14), *T. forficatus* (3), *T. savana* (3), *T. tyrannus* (3), *T. dominicensis,* and *T. caudifasciatus.* The remainder of the 33 species in the kingbird group are not currently available as spirit specimens.

Comparisons were made with the following tyrannid species: *Platyrinchus coronatus, Todirostrum cinereum, Tolmomyias sulphurescens, Camptostoma obsoletum, Elaenia flavogaster, Mionectes oleagineus, Phaeomyias murina, Lophotriccus galeatus, Contopus virens* (2), *Empidonax virescens, Sayornis phoebe* (2), *Pyrocephalus rubinus, Fluvicola pica, Machetornis rixosus, Attila spadiceus,* and *Myiarchus crinitus* (2). Certain muscles were examined in three additional specimens of *Contopus virens,* 13 of *Sayornis phoebe,* and in *Hirundinea ferruginea,* and *Agriornis livida.* These 18 non-kingbird species were chosen to represent a broad spectrum of forms within the Tyrannidae. Collection data for these specimens may be found in McKitrick (manuscript). The descriptions of muscles refer to *Tyrannus melancholicus,* with differences for other species as noted. Anatomical nomenclature follows Baumel et al. (1979), and abbreviations are from Zusi and Bentz (1984).

Abbreviations for museums from which specimens were borrowed are as follows: AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; FMNH, Field Museum of Natural History; KU, University of Kansas; LSU, Louisiana State University; USNM, National Museum of Natural History; YPM, Peabody Museum, Yale University.

Dissections were made with a Wild stereomicroscope at magnifications of 6×, 12×, and 25×, with the use of iodine stain (Bock and Shear, 1972) to enhance visibility of muscle fibers. Preliminary drawings were prepared with the aid of a camera lucida microscope attachment.

The term "kingbird," as used in this paper, refers to any of the 33 species in the kingbird group. Reference may be made to muscular conditions occurring in "a species" when only a single specimen was dissected; this is simply a space-saving construct.

HINDLIMB MUSCLES

M. iliotibialis cranialis (Figs. 1, 2, 9:ICR) is a narrow, fan-shaped muscle that approaches a parallel-fibered condition. It has a wide origin by an aponeurosis from the spinous processes of the thoracic vertebrae and by fleshy fibers from the lateral margin of the Ala preacetabularis ilii. It narrows as it passes distomediad, and inserts by a short tendon on the craniomedial surface of the head of the tibiotarsus.

The other species examined are as described for *Tyrannus melancholicus.*

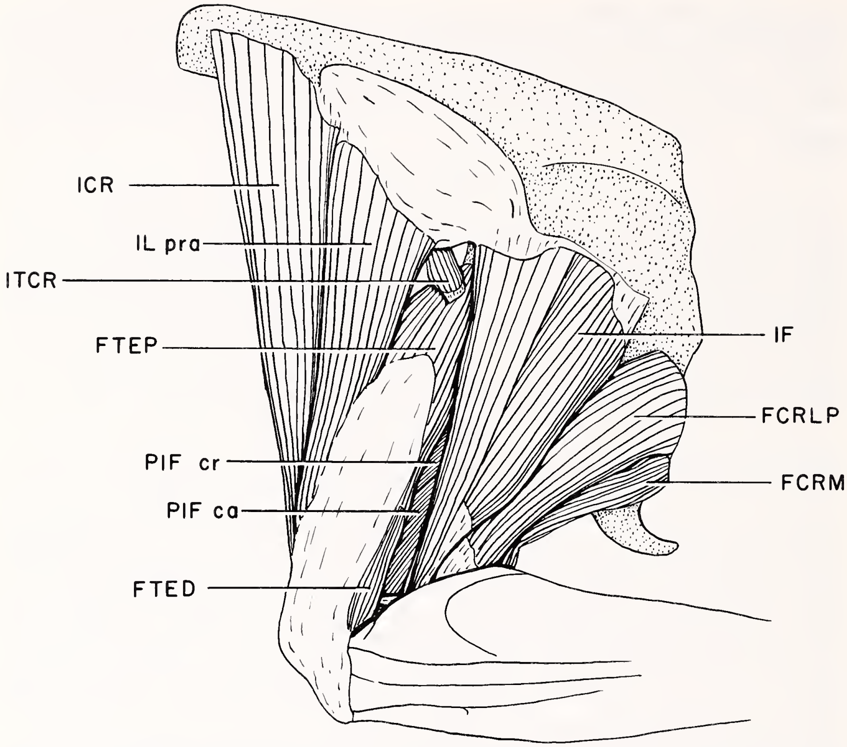

Fig. 1.—Superficial muscles of the lateral surface of the thigh in *Tyrannus melancholicus* AMNH 6697. Abbreviations for all figures: CF, M. caudofemoralis; EDL, M. extensor digitorum longus; EHL, M. extensor hallucis longus; FB, M. fibularis brevis; FCRLA, M. flexor cruris lateralis pars accessoria; FCRLP, M. flexor cruris lateralis pars pelvica; FCRM, M. flexor cruris medialis; FDL fe, M. flexor digitorum longus, femoral head; FDL fi, M. flexor digitorum longus, fibular head; FDL t, M. flexor digitorum longus, tibial head; FHB, M. flexor hallucis brevis; FHL, M. flexor hallucis longus; FL, M. fibularis longus; FPD2, M. flexor perforatus digiti II; FPD3, M. flexor perforatus digiti III; FPD4, M. flexor perforatus digiti IV; FPPD2, M. flexor perforans et perforatus digiti II; FPPD3, M. flexor perforans et perforatus digiti III; FTED, M. femorotibialis externus pars distalis; FTEP, M. femorotibialis externus pars proximalis; FTI, M. femorotibialis internus; FTM, M. femorotibialis medialis; GI, M. gastrocnemius pars intermedius; GL, M. gastrocnemius pars lateralis; GM, M. gastrocnemius pars medialis; ICR, M. iliotibialis cranialis; IF, M. iliofibularis; IFI, M. iliofemoralis internus; IL, M. iliotibialis lateralis; IL pa, M. iliotibialis lateralis pars postacetabularis; IL pra, M. iliotibialis lateralis pars preacetabularis; ISF, M. ischiofemoralis; ITCA, M. iliotrochantericus caudalis; ITCR, M. iliotrochantericus cranialis; ITM, M. iliotrochantericus medialis; OLD, M. obturatorius lateralis dorsalis; OLV, M. obturatorius lateralis ventralis; OM, M. obturatorius medialis; PIF ca, M. pubo-ischio-femoralis pars caudalis; PIF cr, M. pubo-ischio-femoralis pars cranialis; PL, M. plantaris; TCR, M. tibialis cranialis.

M. iliotibialis lateralis (Figs. 1, 2, 3, 9:IL) is a triangular muscle covering the lateral surface of the thigh between Mm. iliotibialis cranialis and femorotibialis externus, and includes only a preacetabular portion in *Tyrannus melancholicus* (Fig. 1:IL pra). It arises by an aponeurosis from the dorsal and dorsolateral iliac crests. In its distal half it becomes entirely aponeurotic laterally and this aponeurosis is closely applied to the distal half of the lateral surface of M. femorotibialis externus. The tendon of insertion forms part of the superficial layer of the patellar tendon along with that of M. femorotibialis externus. There is no postacetabular portion (IL pa).

An acetabular and postacetabular portion are present in *Conopias inornatus,* with a slight gap between the two at the level of the cranial end of the ilioischiadic foramen. A narrow, strap-shaped postacetabular portion, arising by an aponeurosis from the dorsolateral iliac crest cranial to M. flexor cruris lateralis, is present in *Myiodynastes maculatus* CM 363 and CM 1402 (Fig. 2:IL pa), in which it is separated from the preacetabular portion by a wide gap, but it is absent in *M. maculatus* CM 4452, LSU 108693, and LSU 111091. It is present in *Myiodynastes bairdii* LSU 100526 but apparently absent in *M. bairdii* USNM 50913, although the latter specimen was exceptionally decomposed. *Megarynchus pitangua* KU 56828 possesses the postacetabular portion but *M. pitangua* CM 529 lacks it. Two specimens of *Pitangus sulphuratus,* CM 4094 and LSU 31688, possess the postacetabular portion (see Fig. 3), but five, CM 928, 3793, 3846, 4224, and LSU 31689, lack it. In *Conopias trivirgata* (2 specimens), *Myiodynastes luteiventris* (4), *Pitangus lictor* (1), and all other kingbird species examined, only the preacetabular portion is present and the muscle is as described for *Tyrannus melancholicus.*

The following non-kingbird tyrannids possess a narrow postacetabular portion: *Camptostoma obsoletum, Elaenia flavogaster, Phaeomyias murina, Lophotriccus galeatus, Fluvicola pica, Machetornis rixosus,* and *Attila spadiceus.* In *Todirostrum cinereum* and *Platyrinchus coronatus* there are both an acetabular and a postacetabular portion, that is, the muscle is continuous across the lateral surface of the thigh.

Of 15 specimens of *Sayornis phoebe* examined, one (KU 046413) has a slender postacetabular portion on the left side, but not on the right.

These data are summarized in Table 1.

M. iliofibularis (Figs. 1, 2, 3:IF) is a large, triangular muscle lying caudal to M. femorotibialis externus, and is entirely exposed in *Tyrannus melancholicus,* not lying deep to M. iliotibialis lateralis as in many passerines because there is no postacetabular portion of M. iliotibialis lateralis present. The cranial third of the muscle arises by an

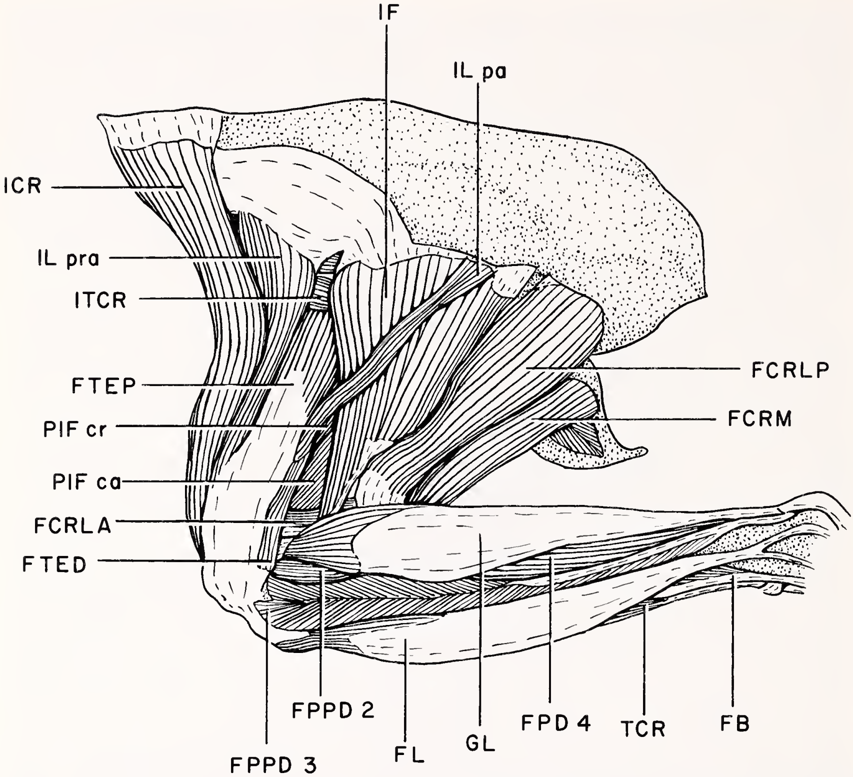

Fig. 2.—Superficial muscles of the lateral surface of the thigh and crus in *Myiodynastes maculatus* KU 56828. See Fig. 1 for abbreviations.

aponeurosis on the dorsal iliac crest dorsal to the acetabulum, sharing a common border dorsally with the aponeurosis by which M. iliotibialis lateralis arises; the central third arises fleshy on the dorsal border of the ilioischiadic fenestra, and the caudal third by a tendinous sheet from the dorsolateral iliac crest just caudal to the ilioischiadic fenestra. The very stout tendon of insertion passes between the lateral and intermediate bellies of M. gastrocnemius and through the biceps loop to insert on a tubercle on the caudal surface of the fibula.

In those species possessing a postacetabular portion of M. iliotibialis lateralis, part of M. iliofibularis lies deep to it.

On the left side of *Pitangus sulphuratus* CM 4094 there is an additional, cranial "head" arising fleshy from the lateral surface of the shaft of the femur (Fig. 3), immediately adjacent to the origin of M. femo-

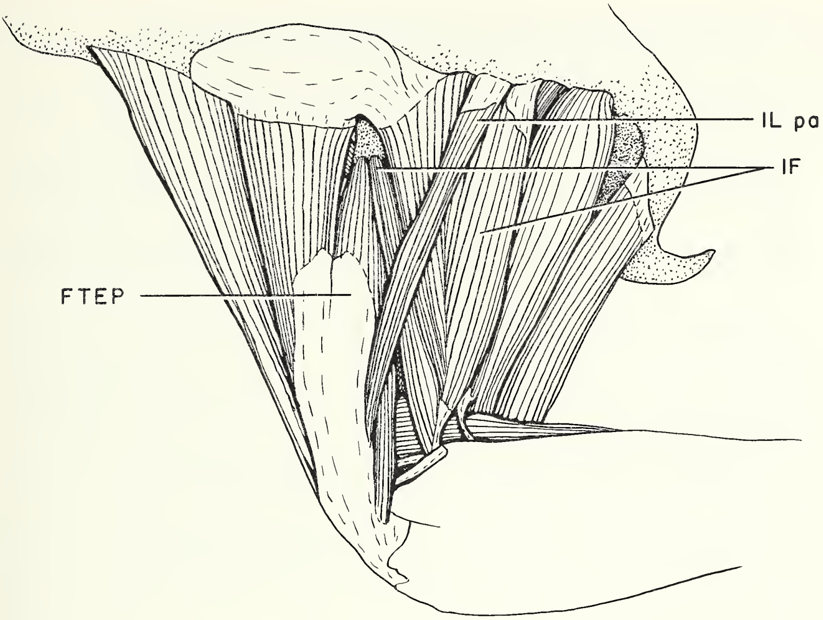

Fig. 3.—Developmental anomaly in *Pitangus sulphuratus* CM 4094. See Fig. 1 for abbreviations.

rotibialis externus (about an eighth of the way down). It joins the main belly of M. iliofibularis medially and fuses with it two-thirds to three-fourths of the way down the length of the belly. The fibers contributing to this additional head appear to be derived from the medial surface of the main belly of M. iliofibularis. On the right side of the specimen a similar situation obtains but the cranial head is slightly narrower than that on the left side, and the cranial fibers of the main belly extend farther craniad and therefore partly overlie the cranial head. The caudal portion of the proximal end of M. femorotibialis externus is slightly reduced in width, suggesting that M. iliofibularis may have developed earlier and usurped that portion of the femoral shaft usually occupied by M. femorotibialis externus. This developmental anomaly apparently has a genetic basis, as it is bilateral. It may have arisen via abnormal enlargement of the premuscle mesenchymal mass, possibly due to a mutation affecting growth rate, and by extending beyond its normal boundaries the muscle achieved an origin from a skeletal element not usually involved. This kind of anomaly has evidently never been described for birds; it may illustrate a mechanism for evolutionary change in muscle attachments.

Table 1.—*Variations in six hindlimb muscles in the Tyrannidae.*[1]

Specimen	IL PA	G PB	G L	G M	EDL		FPPD3		FPD2	FPD3
					b	u	b	u		
Pitangus lictor AMNH 8528	–	–	1/2	3/4	1/2	2/3	1/2	7/8	2/3	3/4
Pitangus sulphuratus CM 928	–	–	1/2	2/3	1/2	3/4	1/2	2/3	1/2	3/4
Pitangus sulphuratus CM 3793	–	–	1/2	2/3	1/2	2/3	1/3	1/2	1/2	3/4
Pitangus sulphuratus CM 3846	–	–	1/2	3/4	1/2	3/4	1/2	2/3	2/3	3/4
Pitangus sulphuratus CM 4094	+	–	1/2	2/3	1/2	2/3	1/3	3/4	2/3	2/3
Pitangus sulphuratus CM 4224	–	–	1/2	2/3	1/2	3/4	1/3	3/4	1/2	2/3
Pitangus sulphuratus LSU 31688	+	–	/	/	/	/	/	/	/	/
Pitangus sulphuratus LSU 31689	–	–	/	/	/	/	/	/	/	/
Megarynchus pitangua CM 529	–	–	1/2	2/3	2/3	3/4	1/2	2/3	1/2	3/4
Megarynchus pitangua KU 56828	+	–	3/4	3/4	7/8	~1	1/2	3/4	1/2	~1
Myiozetetes luteiventris LSU 114492	–	–	1/2	3/4	1/2	3/4	1/3	3/4	2/3	3/4
Myiozetetes cayanensis CM 1233	–	–	/	/	1/2	3/4	1/2	2/3	1/2	1/2
Myiozetetes cayanensis CM 1747	–	–	/	2/3	2/3	~1	1/3	3/4	1/2	1/2
Myiozetetes cayanensis USNM 504542	–	–	1/2	2/3	2/3	7/8	1/2	7/8	3/4	7/8
Myiozetetes cayanensis USNM 504545	–	–	2/3	3/4	1/2	3/4	1/2	7/8	2/3	3/4
Myiozetetes similis CM 921	–	–	1/2	2/3	1/3	3/4	1/2	3/4	1/2	1/2
Myiozetetes similis CM 927	–	–	/	/	1/2	3/4	1/3	3/4	2/3	3/4
Myiozetetes similis CM 3847	–	–	1/2	2/3	1/2	2/3	1/3	2/3	1/2	2/3
Myiozetetes similis CM 3848	–	–	1/2	2/3	1/2	2/3	1/3	3/4	2/3	2/3
Myiozetetes similis CM 3857	–	–	1/2	3/4	1/2	3/4	1/3	3/4	2/3	2/3
Myiozetetes similis CM 4119	–	–	1/2	3/4	1/2	3/4	1/3	3/4	2/3	2/3
Myiozetetes similis CM 4120	–	–	1/2	3/4	1/2	~1	1/3	2/3	2/3	2/3
Myiozetetes similis CM 4301	–	–	1/2	2/3	1/2	2/3	1/3	2/3	2/3	2/3
Myiozetetes similis CM 4302	–	–	1/2	2/3	1/2	2/3	1/3	2/3	1/2	2/3
Myiozetetes similis CM 4475	–	–	1/2	3/4	1/2	3/4	1/2	3/4	3/4	3/4
Myiozetetes similis LSU 31686	–	–	/	/	/	/	/	/	/	/
Myiozetetes similis LSU 63738	–	–	/	/	/	/	/	/	/	/
Myiozetetes similis LSU 114491	–	–	/	/	/	/	/	/	/	/
Myiozetetes similis USNM 504551	–	–	/	/	1/2	3/4	1/2	3/4	2/3	3/4
Myiozetetes similis USNM 506248	–	–	1/2	3/4	1/2	3/4	1/2	3/4	2/3	3/4

Table 1.—*Continued.*

Specimen	IL PA	G PB	G L	G M	EDL		FPPD3		FPD2	FPD3
					b	u	b	u		
Myiozetes granadensis LSU 31687	–	–	1/2	2/3	1/2	3/4	1/2	2/3	3/4	3/4
Conopias inornatus CM 541	+	+	1/2	2/3	1/2	~1	1/2	2/3	1/2	3/4
Conopias parva CM 1784	–	–	1/2	2/3	1/2	~1	1/2	2/3	2/3	3/4
Conopias trivirgata YPM 2639	–	+	1/2	2/3	2/3	0	1/2	2/3	1/2	2/3
Conopias trivirgata YPM 2640	–	+	1/2	1/2	1/3	1/2	1/3	1/2	1/3	1/2
Myiodynastes luteiventris AMNH 6696	–	–	1/2	2/3	1/2	~1	1/2	2/3	1/2	7/8
Myiodynastes luteiventris CM 3979	–	–	1/2	3/4	1/2	~1	1/2	3/4	2/3	~1
Myiodynastes luteiventris CM 4191	–	–	1/2	3/4	1/2	~1	1/2	3/4	2/3	~1
Myiodynastes luteiventris CM 4228	–	–	1/2	3/4	1/2	~1	1/2	3/4	2/3	3/4
Myiodynastes bairdii LSU 100526	+	–	1/2	~1	1/2	~1	1/3	3/4	2/3	3/4
Myiodynastes bairdii USNM 50913	–	–	1/2	3/4	1/3	7/8	/	/	3/4	7/8
Myiodynastes maculatus CM 363	+	–	1/2	2/3	1/2	~1	1/2	3/4	2/3	3/4
Myiodynastes maculatus CM 1402	+	–	2/3	~1	1/2	~1	1/2	3/4	1/2	3/4
Myiodynastes maculatus CM 4452	–	–	1/2	3/4	1/2	2/3	1/2	3/4	1/2	~1
Myiodynastes maculatus LSU 108693	–	–	/	/	/	/	/	/	/	/
Myiodynastes maculatus LSU 111091	–	–	/	/	/	/	/	/	/	/
Legatus leucophaius USNM 510867	–	–	1/2	2/3	1/2	~1	1/2	7/8	2/3	~1
Empidonomus varius FMNH 288494	–	–	1/2	2/3	2/3	3/4	1/2	2/3	2/3	3/4
Empidonomus varius FMNH 288497	–	–	1/2	3/4	1/2	2/3	1/2	3/4	2/3	3/4
Empidonomus varius FMNH 288498	–	–	1/2	3/4	1/2	~1	1/2	2/3	2/3	3/4
Empidonomus aurantioatrocristatus AMNH 2462	–	–	1/2	2/3	1/2	2/3	2/3	3/4	1/2	3/4
Tyrannus niveigularis LSU 100525	–	–	1/2	2/3	1/2	2/3	1/2	2/3	1/2	3/4
Tyrannus melancholicus AMNH 6697	–	–	1/3	1/3	1/2	2/3	1/3	2/3	1/2	/
Tyrannus melancholicus CM 345	–	–	1/2	3/4	1/2	3/4	1/2	2/3	1/2	3/4
Tyrannus melancholicus CM 1054	–	–	1/2	2/3	1/2	3/4	1/2	2/3	1/2	2/3
Tyrannus melancholicus CM 1071	–	–	1/2	2/3	1/3	2/3	1/3	1/2	1/2	2/3
Tyrannus melancholicus CM 1785	–	–	1/2	2/3	1/2	3/4	1/2	2/3	1/2	2/3
Tyrannus melancholicus USNM 504538	–	–	1/2	3/4	1/2	2/3	1/2	3/4	2/3	3/4
Tyrannus melancholicus USNM 504539	–	–	1/3	2/3	1/2	2/3	/	/	/	3/4

Table 1.—*Continued.*

Specimen	IL PA	G PB	G L	G M	EDL		FPPD3		FPD2	FPD3
					b	u	b	u		
Tyrannus vociferans USNM 87297	–	–	1/2	2/3	1/2	2/3	1/3	1/2	1/2	3/4
Tyrannus vociferans USNM 87298	–	–	1/2	2/3	1/2	2/3	1/2	2/3	1/2L 3/4R	2/3
Tyrannus crassirostris KU 42008	–	–	1/2	2/3	1/2	~1	1/3	2/3	1/2	3/4
Tyrannus verticalis CM 2871	–	–	1/2	2/3	1/2	~1	1/2	3/4	1/2	~1
Tyrannus verticalis CM 2872	–	–	1/3	2/3	1/2	3/4	1/2	7/8	1/2	3/4
Tyrannus verticalis CM 3360	–	–	1/2	2/3	1/2	~1	1/2	2/3	1/2	2/3
Tyrannus verticalis CM 3361	–	–	1/2	3/4	1/2	3/4	1/2	2/3	1/2	3/4
Tyrannus verticalis CM 3362	–	–	1/2	3/4	1/2	3/4	1/2	2/3	1/2	2/3
Tyrannus verticalis CM 3367	–	–	1/2	2/3	1/2	2/3	1/2	2/3	1/2	2/3
Tyrannus verticalis CM 3368	–	–	1/2	2/3	1/2	~1	1/2	2/3	1/2	2/3
Tyrannus verticalis CM 3369	–	–	1/2	3/4	1/2	3/4	1/3	2/3	1/2	3/4
Tyrannus verticalis CM 3370	–	–	1/2	2/3	1/2	3/4	1/2	2/3	1/2	2/3
Tyrannus verticalis CM 3371	–	–	1/2	2/3	1/2	3/4	1/2	3/4	1/2	2/3
Tyrannus verticalis CM 3372	–	–	1/2	3/4	1/2	~1	1/2	2/3	1/2	3/4
Tyrannus verticalis CM 3373	–	–	1/3	2/3	1/2	~1	1/2	2/3	1/2	2/3
Tyrannus verticalis CM 3374	–	–	2/3	2/3	1/2	~1	1/2	3/4	1/2	3/4
Tyrannus verticalis CM 3375	–	–	1/2	3/4	1/2	~1	1/2	2/3	1/2	3/4
Tyrannus forficatus CM 2232	–	–	1/2	3/4	1/2	3/4	1/2	2/3	1/2	3/4
Tyrannus forficatus CM 3070	–	–	/	3/4	1/2	3/4	1/3	2/3	1/2	3/4
Tyrannus forficatus CM 3085	–	–	1/2	2/3	1/2	2/3	1/2	2/3	1/2	3/4
Tyrannus savana CM 1284	–	–	1/2	2/3	1/2	3/4	1/3	2/3	1/2	2/3
Tyrannus savana CM 3761	–	–	1/3	2/3	1/2	2/3	1/2	2/3	1/2	~1
Tyrannus savana CM 3768	–	–	1/2	2/3	1/2	2/3	1/3	2/3	2/3	2/3
Tyrannus tyrannus CM 2446	–	–	1/2	2/3	1/2	3/4	1/3	2/3	1/2	/
Tyrannus tyrannus CM 2567	–	–	1/2	2/3	1/2	2/3	/	/	/	3/4
Tyrannus tyrannus CM 2863	–	–	/	/	2/3	7/8	1/2	2/3	1/2	3/4
Tyrannus dominicensis USNM 504541	–	–	1/2	2/3	1/2	2/3	1/2	2/3	1/2	2/3
Tyrannus caudifasciatus USNM 291915	–	–	1/2	2/3	1/2	3/4	1/3	3/4	1/2	2/3

Table 1.—*Continued.*

Specimen	IL PA	G PB	G L	G M	EDL		FPPD3		FPD2	FPD3
					b	u	b	u		
Camptostoma obsoletum CM 1390	+	+	1/2	2/3	1/2	3/4	1/2	2/3	1/2	3/4
Elaenia flavogaster CM 1746	+	+	2/3	2/3	1/3	3/4	1/4	3/4	1/2	3/4
Mionectes oleagineus CM 1317	–	+	1/2	2/3	1/2	3/4	1/2	2/3	1/2	3/4
Phaeomyias murina CM 1787	+	–	1/2	2/3	1/3	3/4	1/3	2/3	1/2	3/4
Lophotriccus galeatus CM 1294	+	+	2/3	1/2	1/4	2/3	1/4	1/2	1/2	1/2
Todirostrum cinereum CM 1876	+	+	1/2	2/3	1/2	2/3	1/2	2/3	1/2	2/3
Tolmomyias sulphurescens CM 1136	–	+	1/2	2/3	1/2	3/4	1/2	2/3	2/3	2/3
Platyrinchus coronatus CM 1866	+	+	1/2	2/3	1/2	3/4	1/2	2/3	1/2	3/4
Contopus virens CM 2858	–	–	1/2	2/3	1/2	3/4	1/2	3/4	1/2	2/3
Contopus virens CM 3069	–	–	1/2	2/3	1/4	2/3	/	/	/	2/3
Empidonax virescens CM 2013	–	–	1/2	2/3	1/4	1/2	1/4	2/3	1/2	3/4
Sayornis phoebe CM 2539	–	–	1/2	2/3	1/2	2/3	1/3	1/2	1/2	2/3
Sayornis phoebe CM 2773	–	–	1/2	2/3	1/4	1/2	/	/	1/2	1/2
Sayornis phoebe KU 046413	+ L	/	/	/	/	/	/	/	/	/
Pyrocephalus rubinus CM 1099	–	–	1/2	2/3	1/2	2/3	1/2	2/3	1/2	1/2
Fluvicola pica CM 1285	–	+	2/3	1/2	1/3	1/2	1/3	2/3	1/2	2/3
Maechetornis rixosus CM 528	+	+	1/2	1/2	2/3	/	1/2	2/3	1/2	1/2
Attila spadiceus CM 1073	+	–	1/2	1/2	2/3	/	1/2	2/3	2/3	2/3
Myiarchus crinitus CM 2574	–	–	1/2	3/4	1/2	3/4	1/3	3/4	3/4	3/4
Myiarchus crinitus CM 2861	–	–	1/2	2/3	1/2	3/4	1/2	2/3	1/2	2/3

[1] Abbreviations: IL PA, M. iliotibialis lateralis pars postacetabularis; G PB, M. gastrocnemius, patellar band; G L, M. gastrocnemius lateralis; G M, M. gastrocnemius medialis; EDL, M. extensor digitorum longus; b, bipennate; u, unipennate; FPPD3, M. flexor perforans et perforatus digiti III; FPD2, M. flexor perforatus digiti II; FPD3, M. flexor perforatus digiti III. Numbers refer to the length of the muscle relative to the length of the tibiotarsus; b and u refer to the proportion of the muscle that is bipennate and unipennate relative to the length of the tibiotarsus; + and – denote presence and absence; /, data not taken; ~, approximately; L & R, left & right.

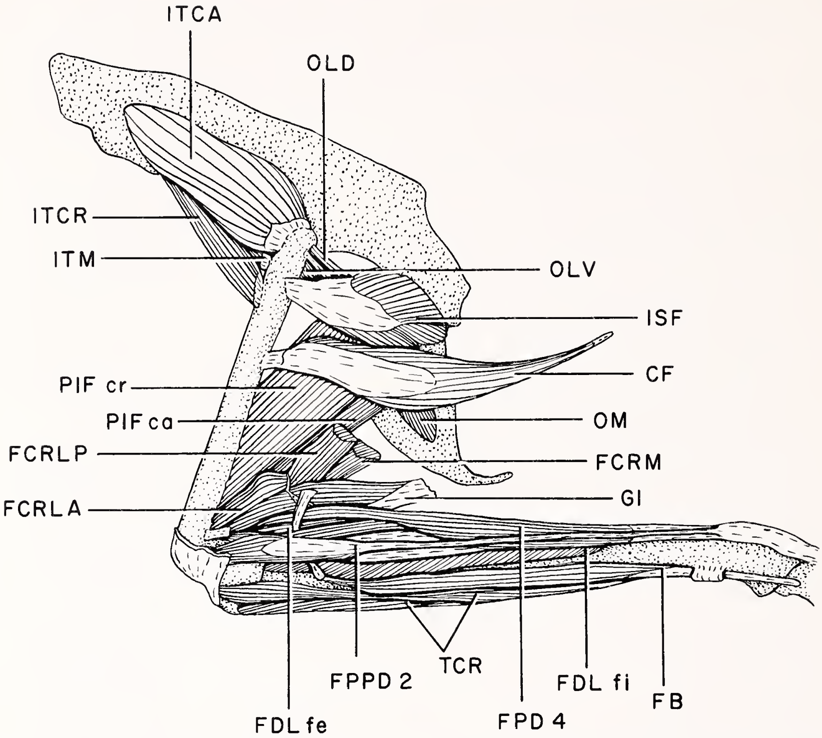

Fig. 4.—Second layer of muscles on the lateral surface of the thigh and crus in *Tyrannus verticalis* CM 3060. See Fig. 1 for abbreviations.

The other six specimens of *Pitangus sulphuratus* examined have the normal condition as described for *Tyrannus melancholicus* above, and there is little variation in this muscle in the other kingbird species examined.

In *Platyrinchus coronatus* and *Todirostrum cinereum* there is a slight gap between the cranial and caudal fiber groups, exposing the ilioischiadic foramen.

M. iliotrochantericus caudalis (Fig. 4:ITCA) is a large, oval, fan-shaped muscle lying in the preacetabular depression (Fossa iliaca dorsalis of the ala preacetabularis ilii). It arises fleshy on the lateral surface of the ilium and the dorsal iliac crest; the aponeurosis giving rise to M. iliotibialis lateralis covers the surface of the muscle. It inserts by a short, stout tendon on the lateral surface of the trochanter of the femur.

The other species examined are as described for *Tyrannus melancholicus*.

M. iliotrochantericus cranialis (Figs. 1, 2, 4, 9, 10:ITCR) is a small muscle, slightly wider at its origin than at its insertion, arising fleshy from the ventrolateral border of the central third of the preacetabular ilium just cranial to the origin of M. iliotrochantericus medius. It passes caudoventrad to insert by a thin, tendinous sheet on the craniolateral surface of the femur just distal to the insertion of M. iliotrochantericus medius.

The other species examined are as described for *Tyrannus melancholicus.*

M. iliotrochantericus medius (Figs. 4, 9, 10:ITM) is a tiny, essentially parallel-fibered muscle having a fleshy origin from the ventrolateral border of the preacetabular ilium caudal to the origin of M. iliotrochantericus cranialis. It passes caudoventrad to insert by a delicate tendon on the craniolateral surface of the femur, proximal to the insertion of M. iliotrochantericus cranialis.

The other species examined are as described for *Tyrannus melancholicus.*

M. iliofemoralis internus (Figs. 9, 10:IFI) is a tiny, parallel-fibered muscle arising fleshy from the ventral border of the preacetabular ilium, caudomedial to the origin of M. iliotrochantericus medius. It passes caudoventrad to insert fleshy on the caudomedial surface of the femur proximal to the origin of M. femorotibialis internus.

The other species examined are as described for *Tyrannus melancholicus* except that in two of 14 specimens of *T. verticalis* (CM 2872 and 3360) the muscle was more slender than usual.

M. femorotibialis externus (Figs. 1, 2, 3:FTE) includes proximal and distal heads. Pars proximalis (FTEP) is parallel-fibered and arises fleshy on the craniolateral, lateral, and caudolateral surfaces of the femoral shaft just distal to the head of the femur. The tendon of insertion arises as an aponeurosis on the proximal fourth of the belly and inserts as a deeper layer of the patellar ligament. Pars distalis (FTED) is unipennate and arises fleshy on the lateral surface of the femoral shaft about a third of the way down and is partially fused along its cranial border with pars proximalis. The tendon of insertion arises as an aponeurosis on the lateral surface of the belly in its proximal portion and inserts on the patellar ligament.

The other species examined are as described for *Tyrannus melancholicus.*

M. femorotibialis medius (Figs. 9, 10:FTM) is a unipennate muscle arising by a narrow tendon on the medial and craniomedial surface of the femoral shaft between Mm. iliotrochantericus cranialis and iliofemoralis internus, and fleshy along the length of the femoral shaft. The tendon of insertion arises as an aponeurosis on the medial surface of the belly in its proximal quarter and forms the deeper, medial layer of the patellar ligament. The common border of Mm. femorotibialis externus and femorotibialis medius is usually indistinct.

The other species examined are as described for *Tyrannus melancholicus.*

M. femorotibialis internus (Figs. 9, 10:FTI) lies between Mm. femorotibialis medius and pubo-ischio-femoralis on the medial surface of the thigh. It is unipennate and arises fleshy on the distal ⅞ of the femoral shaft. The belly is narrower at its origin than at its insertion. The tendon of insertion arises as an aponeurosis in the proximal fourth of the belly and inserts on the caudal margin of the apex of the cranial cnemial crest of the tibiotarsus.

In the other species examined this muscle is as described for *Tyrannus melancholicus,* except that in *Conopias trivirgatus* YPM 2639 it arises on the distal two-thirds of the femur.

M. flexor cruris lateralis (Figs. 1, 2, 4, 12, 13, 14:FCRL) is composed of two bellies in *Tyrannus melancholicus*: pars pelvica and pars accessoria. Pars pelvica (FCRLP) is a broad, parallel-fibered muscle arising by tendinous fibers from the caudal third of the crista iliaca dorsolateralis, caudal and superficial to the insertion of M. ischiofemoralis, and by a tendinous sheet from the first caudal vertebra. It passes distad to give rise to a cranial and a caudal branch. The caudal branch inserts by a flat tendon (tendon M) on the lateral surface of M. flexor cruris medialis proximal to the beginning of the latter's tendon of insertion. The cranial fibers give rise to a narrow tendon, tendon G, which inserts broadly on the lateral surface of M. gastrocnemius pars intermedia. A small, strap-shaped belly, pars accessoria (FCRLA), arises from tendon G distal to the latter's origin such that pars accessoria and pelvica are separated by a gap. Pars accessoria extends distad the entire length of tendon G. It inserts fleshy on the caudolateral surface of the femoral shaft and in the popliteal region of the femur, superficial to the insertion of M. pubo-ischio-femoralis pars cranialis. Because of its somewhat extensive insertion, pars accessoria has the appearance of being divided into two parts, one inserting on the lateral surface of the femoral shaft and one in the popliteal region. In some species (see below) this division is real, due to an actual gap in the fibers arising on tendon G.

In two specimens, CM 1071 and USNM 504538, pars accessoria is slightly reduced proximally.

The above description of *Tyrannus melancholicus* is based on 7 specimens: AMNH 6697, CM 345, 1054, 1071, 1785, USNM 504538, and 504539.

M. flexor cruris lateralis varies considerably among and within species. These variations are primarily in pars accessoria and its connection with pars pelvica, and are described in detail in another paper (McKitrick, manuscript). Figs. 12–14 illustrate the extreme of robustness in the muscle, the intermediate condition where tendon G is exposed, and the extreme of reduction in which pars accessoria and tendon G are absent, leaving only pars pelvica. In addition to the variations in pars accessoria, the following occur: In *Platyrinchus coronatus* tendon M joins M. flexor cruris lateralis at the proximal end of the latter's tendon of insertion; in *Todirostrum cinereum* tendon M does not fuse with M. flexor cruris lateralis at all, but rather inserts directly on the tibiotarsus. In *Sayornis phoebe* and *Contopus virens* pars pelvica is very narrow (Figs. 13, 14).

M. flexor cruris medialis (Figs. 1, 2, 4, 9, 10, 12, 13, 14:FCRM) is a parallel-fibered muscle lying medial and slightly caudal to M. flexor cruris lateralis. It arises by fleshy and semitendinous fibers from the lateral surface of the caudal portion of the Ala ischii and the Processus terminalis ischii. It passes distad and gives rise to a tendinous sheet that attaches on the proximomedial surface of the tibiotarsus. The muscle is joined by a tendon (tendon M) from M. flexor cruris lateralis—see description for that muscle.

The other species examined are as described for *Tyrannus melancholicus,* except that in *Todirostrum cinereum* this muscle is very narrow.

M. caudofemoralis (Figs. 4, 10:CF) is a spindle-shaped muscle lying ventral to M. ischiofemoralis and deep to M. iliofibularis on the lateral surface of the thigh. It arises by a very narrow tendon on the pygostyle, and passes fleshy craniad to insert by a narrow tendon on the caudal surface of the femoral shaft about a fourth the way down.

The other species examined are similar to *Tyrannus melancholicus,* except that in *Myiodynastes bairdii* LSU 100526 and *Tyrannus dominicensis* USNM 504541 the insertion is partly fleshy.

M. ischiofemoralis (Fig. 4:ISF) is a fan-shaped muscle lying deep to M. iliofibularis. It arises fleshy from the ventral surface of the caudal two-thirds of the Crista iliaca dorsolateralis, from the Lamina ischiadica of the ilium, and the caudal portion of the Ala ischii. The stout tendon of insertion arises as an aponeurosis on the lateral surface of the belly in its proximal third, and the fibers arising at the dorsal and caudodorsal border of the Foramen ilioischiadicum actually insert on the surface of this aponeurosis. The muscle proceeds craniad and narrows to insert on the femoral shaft just distal to the head of the femur.

The other species examined are as described for *Tyrannus melancholicus.*

M. obturatorius lateralis (Fig. 4) is composed of separate tiny dorsal and ventral heads lying deep to M. ischiofemoralis. Pars dorsalis (OLD) arises fleshy on the caudoventral border of the ilioischiadic foramen and from the lateral surface of the ischium ventral to the ilioischiadic foramen. It is of medium size according to Raikow's (1978) terminology

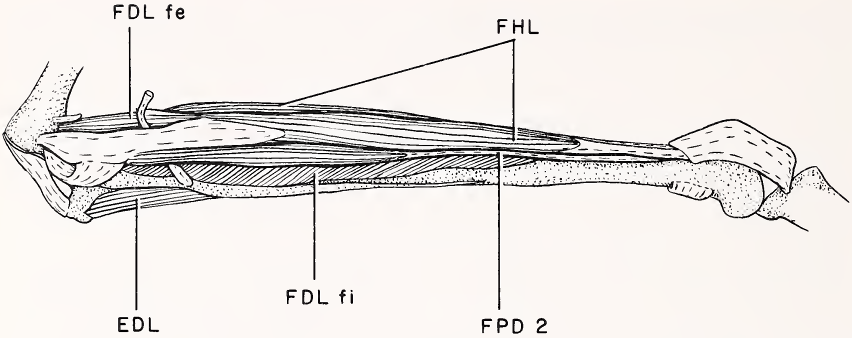

Fig. 5.—Third layer of muscles on the lateral surface of the crus in *Tyrannus melancholicus* CM 1785. See Fig. 1 for abbreviations.

in that it lies between the obturator foramen and the ilioischiadic foramen. It inserts by a tiny, stout tendon on the caudal surface of the head of the femur just cranial to the tendon of insertion of M. obturatorius medialis. Pars ventralis (OLV) arises fleshy from the lateral surface of the ischium ventral to the obturator foramen, just ventral to the tendon of insertion of M. obturatorius medialis. It is about equal in size to pars dorsalis. It inserts fleshy on the caudomedial surface of the femur, distal (ventral) to the insertion of M. obturatorius medialis.

The other species examined are as described for *Tyrannus melancholicus.*

M. obturatorius medialis (Figs. 4, 9, 10:OM) is an ovate, bipennate muscle lying in the ischiopubic fenestra. It arises fleshy from the ischium and pubis which form the rim of the fenestra. The fibers converge on a central tendon that passes through the obturator foramen and inserts on the caudal surface of the head of the femur.

The other species examined are as described for *Tyrannus melancholicus.*

M. pubo-ischio-femoralis (Figs. 1, 2, 4, 9, 10:PIF) is composed of adjacent parallel-fibered cranial and caudal bellies arising by a tendinous sheet on the lateral surface of the Ala ischii. Pars cranialis (PIF cr) passes craniad to insert fleshy on the distocaudal two-thirds of the femoral shaft. Pars caudalis (PIF ca) proceeds craniad also but passes medial to M. gastrocnemius pars intermedia and inserts by tendinous fibers on the medial portion of the proximocranial surface of that muscle. Some fibers of pars caudalis insert fleshy on the medial surface of the medial condyle of the femur, with a few fibers inserting fleshy on the caudomedial surface of the femoral shaft. The two bellies are covered proximomedially by a single aponeurosis.

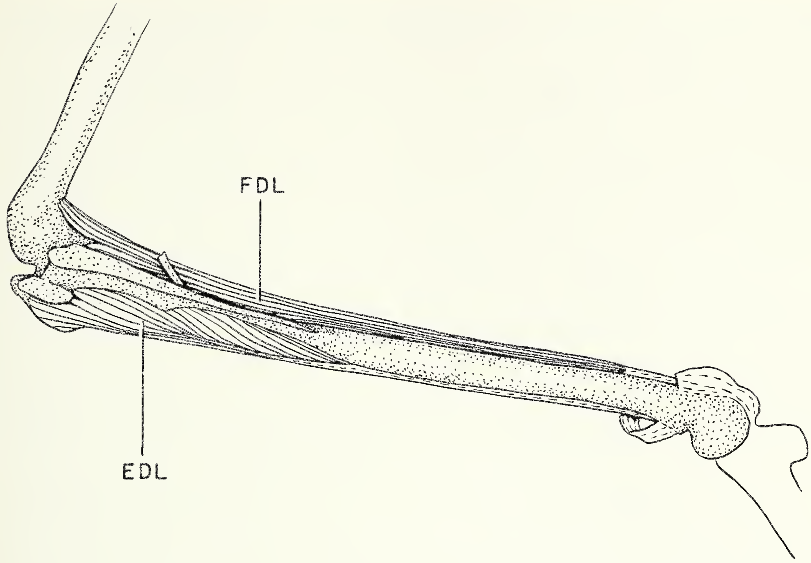

Fig. 6.—Deep layer of muscles on the lateral surface of the crus in *Tyrannus melancholicus* CM 1785. See Fig. 1 for abbreviations.

The other kingbird species examined are as described for *Tyrannus melancholicus.*

The muscle is relatively narrow in *Platyrinchus coronatus, Todirostrum cinereum, Tolmomyias sulphurescens, Lophotriccus galeatus,* and *Mionectes oleagineous,* but otherwise as described for *T. melancholicus.*

M. tibialis cranialis (Figs. 2, 4, 9:TCR) is composed of a tibial and a femoral head. The tibial head is bipennate and arises fleshy from the lateral surface of the cranial cnemial crest, the patellar crest and the cranial surface of the lateral cnemial crest, and by tendinous and semitendinous fibers from the caudal surface of the lateral cnemial crest. The femoral head is bipennate and arises by a stout tendon from the cranial surface of the lateral condyle of the femur, and by a smaller tendon arising from the ligamentous tissue surrounding the head of the fibula. The tibial and femoral heads fuse to form a common belly two-thirds of the way down the crus; this belly narrows to a stout tendon that passes through the transverse ligament on the cranial surface of the tibiotarsus. It crosses the articular surface to insert on the Tuberositas M. tibialis cranialis on the dorsal surface of the tarsometatarsus.

The other species examined are as described for *Tyrannus melancholicus.*

M. extensor digitorum longus (Figs. 5, 6, 10, 11:EDL) is a bipennate muscle lying deep to M. tibialis cranialis. It arises fleshy from the medial and lateral surfaces of the cranial cnemial crest, the patellar crest, the cranial surface of the lateral cnemial crest and the lateral surface of the proximal fourth of the tibiotarsus. The belly is bipennate to about half way down the cranial surface of the crus, then continues unipennate to about two-thirds the way down the crus, and narrows to a tendon. The tendon passes through the transverse ligament, crosses the articular surface and is bound to the dorsal (cranial) surface of the medial cotyla of the tarsometatarsus by a ligament. The tendon passes down the dorsal surface of the tarsometatarsus. It gives off a lateral and a medial branch to digits IV and II respectively, with the main, central branch going to digit III.

The branch to digit II bifurcates, with the lateral branch inserting on the proximodorsal surface of the ungual phalanx and the medial branch on the proximodorsal surface of phalanx 2.

The branch to digit III trifurcates, with the lateral and medial branches inserting together on the proximodorsal surface of the ungual phalanx and the intermediate branch on the proximodorsal surface of phalanx 2.

The branch to digit IV bifurcates at the level of the middle of phalanx 2; the lateral branch inserts on the proximodorsal surface of the ungual phalanx and the medial branch on the proximodorsal surface of the ungual phalanx and the medial branch on the proximodorsal surface of phalanx 4.

This muscle varies in length within and among the species examined. The variation is summarized in Table 1.

M. fibularis longus (Fig. 2:FL) is the most superficial muscle on the craniolateral surface of the crus, lying superficial to M. tibialis cranialis. It arises by a tendinous sheet from the cranial and lateral cnemial and patellar crests of the tibiotarsus, with a tendinous attachment to the caudal border of the lateral cnemial crest. The bipennate belly passes caudal to the belly of M. tibialis cranialis and becomes tendinous at the distal end of the tibiotarsus. The tendon bifurcates, with the main branch inserting on the proximolateral corner of the tibial cartilage, and a fine branch passing across the intertarsal joint lateral to the tendon of M. fibularis brevis, joining the tendon of M. flexor perforatus digiti III on the lateroplantar surface of the tarsometatarsus.

The other species examined are as described for *Tyrannus melancholicus.*

M. fibularis brevis (Figs. 2, 4:FB) is a narrow, bipennate muscle lying caudal to M. tibialis cranialis on the lateral surface of the crus and extending nearly the length of the crus. It arises fleshy on the cranial surface of the distal two-thirds of the fibula. The stout tendon of insertion surfaces in the distal quarter of the belly and is held by a retinaculum against the distal end of the tibiotarsus. The tendon inserts on the lateral surface of the lateral cotyla of the tarsometatarsus.

The other species examined are as described for *Tyrannus melancholicus.*

M. gastrocnemius (Figs. 2, 4, 9, 10, 12, 13, 14) is composed of three separate bellies of origin. Pars lateralis (GL) is spindle-shaped and is the most superficial muscle on the caudolateral surface of the crus, arising by a stout tendon from the lateral epicondyle of the femur. This tendon is partially fused on its medial surface with the lateral arm of the biceps loop. The belly extends half way down the crus and is covered by an aponeurosis in its distal half. The tendon of insertion arises from this aponeurosis and fuses with that of pars intermedia and pars medialis. The common tendon (Achilles tendon) is lightly bound to the joint capsule and to the hypotarsus and inserts extensively on the plantar ridge of the tarsometatarsus.

Pars intermedia (GI) is a small, essentially parallel-fibered muscle arising by a small, stout tendon on the caudomedial surface of the medial condyle of the femur, and by fleshy fibers in the popliteal region. It extends a quarter to a third of the way down the crus and then becomes a flat, tendinous sheet that joins the tendon of insertion of pars lateralis to form the broad Achilles tendon.

Pars medialis (GM) arises semitendinous on the cranial cnemial crest of the tibiotarsus, and by a broad, flat tendon on the medial surface of the crest. The tendon of insertion arises as an aponeurosis in the proximal quarter of the belly; the belly extends two-thirds the way down the crus before becoming completely tendinous. It joins the tendon of pars lateralis and pars intermedia to form the Achilles tendon.

There is little variation among the species examined in pars intermedia, but pars medialis varies in possessing a deep head, a superficial head and a patellar band in some forms. The deep head arises fleshy from the medial surface of the head of the tibiotarsus, and where present the superficial head arises fleshy on the patellar tendon, where it may form a patellar band (see Raikow, 1978:23). A small patellar band is present in *Conopias inornatus* CM 541 and *C. trivirgata* YPM 2639, but the superficial head is poorly developed. A poorly developed superficial head is present in *Myiodynastes luteiventris* CM 3979 (but not the other three specimens of this species), *Legatus leucophaius* USNM 510867, *Empidonomus varius* FMNH 288494 and 288497 (but not 288498), and *T. forficatus* CM 3085 as well. A definite superficial head is present in *Pitangus sulphuratus* LSU 31688.

A well developed patellar band is present in *Camptostoma obsoletum, Platyrinchus coronatus, Todirostrum cinereum, Elaenia flavogas-*

ter, Fluvicola pica, and *Lophotriccus galeatus.* A less extensive patellar band is present in *Tolmomyias sulphurescens, Mionectes oleagineus,* and *Machetornis rixosus* (see Table 1).

The lateral and medial bellies may vary in length, both within and among species (see Table 1).

M. plantaris (Figs. 9, 10:PL) is a small, unipennate muscle lying superficial to M. flexor digitorum longus, deep to M. gastrocnemius pars medialis and cranial to M. flexor perforatus digiti III on the medial surface of the crus. It arises by a thin, tendinous sheet on the caudomedial surface of the head of the tibiotarsus and extends about one-fourth the way down the medial surface of the crus before giving rise to a fine tendon which inserts on the proximomedial corner of the tibial cartilage.

The other species examined are as described for *Tyrannus melancholicus.*

M. flexor perforans et perforatus digiti II (Figs. 2, 4:FPPD2) is a unipennate muscle lying deep to M. gastrocnemius pars lateralis on the lateral surface of the crus, caudal to M. flexor perforans et perforatus digiti III, and superficial to M. flexor perforatus digiti II. It arises by a tendinous sheet from the caudoproximal portion of the lateral condyle of the femur, in common with Mm. flexor perforatus digiti II, flexor perforans et perforatus digiti III, and the lateral head of Mm. flexor perforatus digiti IV and flexor hallucis longus. The belly passes less than one-fourth the way down the crus and narrows to a fine tendon which passes through the caudomedial corner of the tibial cartilage and the caudomedial hypotarsal canal, along the plantar surface of the tarsometatarsus, through the articular cartilage at the base of digit II, passing deep to the tendon of M. flexor perforatus digiti II, and superficial to that of M. flexor digitorum longus. It then passes to the plantar side of digit II, where it inserts on the medial surface of the base of phalanx 2.

This muscle varies little among the species examined, except that on the left side of *Myiodynastes bairdii* LSU 100526 there is an extra head, about one-third to one-half the size of the normal head, arising slightly distal to the normal one on the lateral surface of the tendon of insertion. It fuses with M. FPPD3 on the medial surface of same about one-fourth the way down the crus. Some deep fibers of the normal belly likewise insert fleshy on M. FPPD3. Between the two bellies of M. FPPD2 are a few scattered fibers arising on the tendon of insertion of M. FPPD2 and inserting on M. FPPD3.

M. flexor perforans et perforatus digiti III (Fig. 2:FPPD3) lies on the lateral surface of the crus, caudal to M. fibularis longus and cranial to M. flexor perforans et perforatus digiti II. It is composed of a cranial and a caudal head. The cranial head arises by a flat tendon on the lateral cnemial crest of the tibiotarsus and from the patellar tendon. The caudal head arises by a tendinous sheet from the inner surface of the patellar ligament, and from the proximocaudal surface of the lateral condyle of the femur in common with Mm. flexor perforans et perforatus digiti II, flexor perforatus digiti II and the lateral head of Mm. flexor perforatus digiti IV and flexor hallucis longus. The two heads converge on a central tendon. The common belly is bipennate for about half the length of the crus, then continues unipennate on the cranial surface of the tendon and extends two-thirds the length of the crus. The tendon of insertion passes through the lateral side of the tibial cartilage, through the caudomedial canal of the hypotarsus, down the plantar surface of the tarsometatarsus, and to the plantar side of digit III. It perforates the tendon of M. flexor perforatus digiti III (as does that of M. flexor digitorum longus) and then bifurcates. The tendon of M. flexor digitorum longus passes between the branches. The two branches insert on the lateral and medial corners of the base of phalanx 3.

This muscle varies in length within and among the species examined. The variation is summarized in Table 1.

M. flexor perforatus digiti II (Fig. 5:FPD2) is a bipennate muscle arising by a tendinous sheet from the caudoproximal surface of the lateral condyle of the femur, in common with Mm. flexor perforans et perforatus digiti II, flexor perforans et perforatus digiti III (caudal head), and the lateral head of Mm. flexor perforatus digiti IV, and flexor hallucis longus. The proximal end of the belly is covered by the tendon of origin of the lateral head of M. flexor perforatus digiti IV. The belly extends about half way down the crus, narrows to a tendon which passes across the lateral surface of the crus, through the lateral side of the tibial cartilage and the craniomedial canal of the hypotarsus, and down the plantar surface of the crus to digit II, where it inserts on the medial surface of the base of the first phalanx.

The belly may vary in length. This variation is summarized in Table 1.

M. flexor perforatus digiti III (Fig. 10:FPD3) is a unipennate muscle lying medial to M. flexor perforatus digiti IV and arising by a stout tendon from the popliteal region of the femur in common with the medial head of M. flexor perforatus digiti IV and the medial head of M. flexor hallucis longus. The belly extends two-thirds the way down the crus and is covered by an aponeurosis for all but the proximalmost portion of its length. It is very closely associated with M. flexor hallucis longus deep to it. The tendon of insertion passes through the lateral side of the tibial cartilage along with that of M. flexor perforatus digiti IV and both tendons pass through the caudolateral canal of the hypotarsus and down the plantar surface of the tarsometatarsus—M.

flexor perforatus digiti III deep to and investing the tendon of M. flexor perforatus digiti IV in the proximal third of the tarsometatarsus. M. flexor perforatus digiti III goes to digit III, at the base of which it bifurcates to permit passage of the tendons of Mm. flexor perforans et perforatus digiti III and flexor digitorum longus. The forks insert on the medial and lateral corners, respectively, of the base of phalanx 2.

The muscle may vary in length. This variation is summarized in Table 1.

M. flexor perforatus digiti IV (Figs. 2, 4, 15:FPD4) is composed of a proximal and a distal head. The proximal head arises by a tendinous sheet in the popliteal region of the femur in common with M. flexor perforatus digiti III and the medial head of M. flexor hallucis longus. The tiny distal head arises by a narrow tendon from the tendinous sheet of origin of Mm. flexor perforatus digiti II, flexor perforans et perforatus digiti II, flexor perforans et perforatus digiti III (caudal head), and flexor hallucis longus (lateral head) on the lateral condyle of the femur. The tendon of the distal head of M. flexor perforatus digiti IV continues distad for two-thirds the length of the belly of the medial head before giving rise to the tiny distal belly. The belly of the proximal head extends about three-fourths the way down the crus, narrows to a tendon which passes through the tibial cartilage laterally, through a caudolateral canal in the hypotarsus along with the tendon of M. flexor perforatus digiti III, and down the plantar surface of the tarsometatarsus to digit IV. At about the middle of the first phalanx the tendon bifurcates to permit passage of the tendon of M. flexor digitorum longus. One branch inserts on the medial corner of the base of phalanx 2, while the larger branch inserts broadly at the base of phalanx 3.

There is no distal head present in *Conopias inornatus.* In this species, Mm. flexor perforatus digiti IV and flexor perforatus digiti III are about the same size and lie side by side on the medial surface of the crus.

The distal head shows a tendency to divide, giving the appearance of two tiny bellies, in *Myiozetetes cayanensis* CM 1233, *M. granadensis* LSU 31687, *Conopias trivirgata* YPM 2639, *Myiodynastes luteiventris* AMNH 6696, *M. bairdii* USNM 50913 (but not LSU 100526), *M. maculatus* CM 4452, *Legatus leucophaius* USNM 510867, *Empidonomus varius* FMNH 288494 and 288497 (but not 288498), and *Tyrannus niveigularis* LSU 100525 (Fig. 14).

In *Machetornis rixosus* there are 2 distinct distal bellies on both sides (Fig. 14), arising by a single tendon in common with Mm. flexor perforans et perforatus digiti II, flexor perforatus digiti II, flexor perforans et perforatus digiti III, and flexor hallucis longus.

The other species examined are as described for *Tyrannus melancholicus.*

M. flexor hallucis longus (Figs. 5, 16:FHL) is composed of a lateral, an intermediate, and a medial head. The lateral head arises by a tendinous sheet on the caudoproximal surface of the lateral condyle of the femur in common with Mm. flexor perforatus digiti II, flexor perforans et perforatus digiti II, and flexor perforatus digiti IV (lateral head), with a branch arising tendinous on the lateral surface of the head of the fibula. The belly itself arises less than one-fourth the way down the crus and passes lateral to the tendon of M. iliofibularis. The small intermediate head arises by a short, narrow tendon from the caudal surface of the distal end of the femoral shaft and by semitendinous fibers on the medial surface of the tendon of origin of the lateral head (Fig. 16b), and passes medial to the tendon of M. iliofibularis. The medial head, largest of the three, arises in common with Mm. flexor perforatus digiti IV (medial head) and flexor perforatus digiti III on the lateral surface of the popliteal fossa by a narrow tendon on the medial surface of the belly, with the fibers on the lateral surface of the belly arising fleshy. The three bellies fuse about one-fourth the way down the crus, giving rise to a flat tendon. This tendon passes through the tibial cartilage and through the central canal in the hypotarsus, down the plantar surface of the tarsometatarsus medial to Metatarsal I, over the articular surface to the hallux where it inserts at the base of the ungual phalanx. At the base of the hallux the tendon of M. flexor hallucis longus is ensheathed in a pulley arising from the tendon of M. flexor hallucis brevis.

The muscle may vary in whether an intermediate head is present (Fig. 16e, and see Table 2).

In *Conopias inornatus* CM 541 the intermediate head is present but does not arise in common with M. flexor perforatus digiti IV since the latter's distal head is absent. The intermediate head is actually composed of two heads itself, the more medial of the two being about twice the width of the other. The two arise side by side on the distal end of the femoral shaft, the medial one by tendinous fibers becoming fleshy distad, the more lateral one by both a tendinous sheet and tendinous fibers becoming fleshy distad.

The intermediate head may arise by a tendon adjacent to the medial head rather than the lateral head in the following (Fig. 16a, and see Table 2). In *Tyrannus verticalis* CM 2871 and 3367, *T. savana* 3768, and *T. forficatus* CM 3085, in which the intermediate head arises medially, the head is tiny and the tendon of origin very slender.

In some species there is a tiny intermediate head arising with the medial head, and a second, miniscule intermediate head arising with the lateral head and fusing with the larger intermediate head (Fig. 16c, and see Table 2). In *T. verticalis* CM 3368 there are two tiny intermediate heads, both arising with the lateral head (Fig. 16d).

Most species examined have the intermediate head arising with the lateral head as in *Tyrannus melancholicus*. These data are summarized in Table 2.

Table 2.—*Variations in M. flexor hallucis longus in the Tyrannidae.*[1]

	FHL			
Specimen	Int. hd.	Int. hd. med. orig.	Int. hd. lat. orig.	Int. hd. split
Pitangus lictor AMNH 8528	−	−	−	−
Pitangus sulphuratus CM 928	−	−	−	−
Pitangus sulphuratus CM 3793	+	+	−	−
Pitangus sulphuratus CM 3846	+	+	−	−
Pitangus sulphuratus CM 4094	+	+	−	−
Pitangus sulphuratus CM 4224	+	+	−	−
Pitangus sulphuratus LSU 31688	+	+	−	−
Pitangus sulphuratus LSU 31689	+	−	+	−
Megarynchus pitangua CM 529	+	−	+	−
Megarynchus pitangua KU 56828	+	−	+	−
Myiozetetes luteiventris LSU 114492	+	+	−	−
Myiozetetes cayanensis CM 1233	+	+	−	−
Myiozetetes cayanensis CM 1747	+	+	−	−
Myiozetetes cayanensis USNM 504542	+	+	−	−
Myiozetetes cayanensis USNM 504545	+	+	−	−
Myiozetetes similis CM 921	+	+	−	−
Myiozetetes similis CM 927	+	+	−	−
Myiozetetes similis CM 3847	+	+	−	−
Myiozetetes similis CM 3848	+	+	−	−
Myiozetetes similis CM 3857	+	+	−	−
Myiozetetes similis CM 4119	+	+	−	−
Myiozetetes similis CM 4120	+	+	−	−
Myiozetetes similis CM 4301	+	+	−	−
Myiozetetes similis CM 4302	+	+	−	−
Myiozetetes similis CM 4475	+	+	−	−
Myiozetetes similis LSU 31686	+	+	−	−
Myiozetetes similis LSU 63738	+	+	−	−
Myiozetetes similis LSU 114491	+	+	−	−
Myiozetetes similis USNM 504551	+	+	−	−
Myiozetetes similis USNM 506248	+	+	−	−
Myiozetetes granadensis LSU 31687	−	−	−	−
Conopias inornatus CM 541	+	?	?	+
Conopias parva CM 1784	+	+ R	+ R	+
Conopias trivirgata YPM 2639	+	+	−	−
Conopias trivirgata YPM 2640	+	+	−	−
Myiodynastes luteiventris AMNH 6696	+	−	+	−
Myiodynastes luteiventris CM 3979	+	+ L	+ L	+
Myiodynastes luteiventris CM 4191	+	−	+	−
Myiodynastes luteiventris CM 4228	+	−	+	−
Myiodynastes bairdii LSU 100526	+	−	+	−
Myiodynastes bairdii USNM 50913	+	−	+	−
Myiodynastes maculatus CM 363	+	−	+	−
Myiodynastes maculatus CM 1402	+	−	+	−
Myiodynastes maculatus CM 4452	+	+ L	+ L	+ L
Myiodynastes maculatus LSU 108693	+	−	+	−
Myiodynastes maculatus LSU 111091	+	−	+	−
Legatus leucophaius USNM 510867	+	+	−	−

Table 2.—*Continued.*

	FHL			
Specimen	Int. hd.	Int. hd. med. orig.	Int. hd. lat. orig.	Int. hd. split
Empidonomus varius FMNH 288494	−	−	−	−
Empidonomus varius FMNH 288497	+	−	+	−
Empidonomus varius FMNH 288498	+	−	+	−
Empidonomus aurantioatrocristatus AMNH 2462	+	−	+	−
Tyrannus niveigularis LSU 100525	+	−	+	−
Tyrannus melancholicus AMNH 6697	+	+	+	+
Tyrannus melancholicus CM 345	+	−	+	−
Tyrannus melancholicus CM 1054	+	−	+	−
Tyrannus melancholicus CM 1071	+	−	+	−
Tyrannus melancholicus CM 1785	+	−	+	−
Tyrannus melancholicus USNM 504538	+	−	+	−
Tyrannus melancholicus USNM 504539	+	−	+	−
Tyrannus vociferans USNM 87297	+	+	+	+
Tyrannus vociferans USNM 87298	+	−	+	−
Tyrannus crassirostris KU 42008	+	+	+	+
Tyrannus verticalis CM 2871	+	+	−	−
Tyrannus verticalis CM 2872	+	+	−	−
Tyrannus verticalis CM 3360	−	−	−	−
Tyrannus verticalis CM 3361	+	+	−	−
Tyrannus verticalis CM 3362	+	+	−	−
Tyrannus verticalis CM 3367	+	+	−	−
Tyrannus verticalis CM 3368	+	−	+	+
Tyrannus verticalis CM 3369	+	+	+	+
Tyrannus verticalis CM 3370	+	+	−	−
Tyrannus verticalis CM 3371	+	+	−	−
Tyrannus verticalis CM 3372	+	+	−	−
Tyrannus verticalis CM 3373	+	+	+	+
Tyrannus verticalis CM 3374	+	+	−	−
Tyrannus verticalis CM 3375	+	+	−	−
Tyrannus forficatus CM 2232	+	−	+	−
Tyrannus forficatus CM 3070	+	−	+	−
Tyrannus forficatus CM 3085	− R	+ L	−	−
Tyrannus savana CM 1284	+	−	+	−
Tyrannus savana CM 3761	−	−	−	−
Tyrannus savana CM 3768	+	+	−	−
Tyrannus tyrannus CM 2446	−	−	−	−
Tyrannus tyrannus CM 2567	−	−	−	−
Tyrannus tyrannus CM 2863	−	−	−	−
Tyrannus dominicensis USNM 504541	−	−	−	−
Tyrannus caudifasciatus USNM 291915	+	−	+	−
Camptostoma obsoletum CM 1390	+	−	+	−
Elaenia flavogaster CM 1746	−	−	−	−
Mionectes oleagineus CM 1317	+	−	+	−
Phaeomyias murina CM 1787	−	−	−	−
Lophotriccus galeatus CM 1294	/	/	/	/
Todirostrum cinereum CM 1876	+	−	+	−
Tolmomyias sulphurescens CM 1136	+	−	+	−

Table 2.—*Continued.*

	FHL			
Specimen	Int. hd.	Int. hd. med. orig.	Int. hd. lat. orig.	Int. hd. split
Platyrinchus coronatus CM 1866	+	−	+	−
Contopus virens CM 2858	+	−	+	−
Contopus virens CM 3069	+	−	+	−
Empidonax virescens CM 2013	+	−	+	−
Sayornis phoebe CM 2539	+	−	+	−
Sayornis phoebe CM 2773	+	−	+	−
Pyrocephalus rubinus CM 1099	+	−	+	−
Fluvicola pica CM 1285	+	−	+	−
Machetornis rixosus CM 528	−	—	—	—
Attila spadiceus CM 1073	+	−	+	−
Myiarchus crinitus CM 2574	+	−	+	−
Myiarchus crinitus CM 2861	+	−	+	−

[1] Abbreviations: FHL, M. flexor hallucis longus; int. hd., intermediate head; med. orig., medial origin; lat. orig., lateral origin; L & R, left & right; + and − denote presence and absence; —, not applicable; /, data not taken. See text for further explanation.

M. flexor digitorum longus (Figs. 4, 5, 6, 7, 10, 11:FDL) is composed of a fibular, a femoral, and a tibial head. The fibular head (FDL fi) arises fleshy on the caudal surface of the fibula beginning at the head. The femoral head (FDL fe) is very large and arises fleshy on the caudal surface of the distal end of the femoral shaft. The tibial head (FDL t) arises fleshy in the proximal half of the caudal surface of the head of the tibiotarsus. The muscle is bipennate, with the fibers of the femoral and tibial heads inserting on a central tendon medially, and the fibers of the fibular head inserting laterally on the central tendon. The belly extends nearly the length of the crus, narrows to a tendon which passes through the medial side of the tibial cartilage, through the craniomedial canal of the hypotarsus (this canal is actually set apart medially from the main hypotarsal corpus), and down the plantar surface of the tarsometatarsus. It bifurcates at the level of the Metatarsal I, sending a branch to digit II. The main branch immediately bifurcates again, the lateral branch going to digit III and the medial branch to digit IV.

The branch to digit II inserts at the base of the ungual phalanx and by an elastic vinculum near the distal end of phalanx 2. The branch to digit III inserts on the base of the ungual phalanx of digit III and by an elastic band near the distal end of phalanx 3. The branch to digit IV inserts at the base of the ungual phalanx of digit IV and by two elastic bands, one at the base of phalanx 4 and one at the distal end of phalanx 4.

Flexor digitorum longus varies among species in the size of the

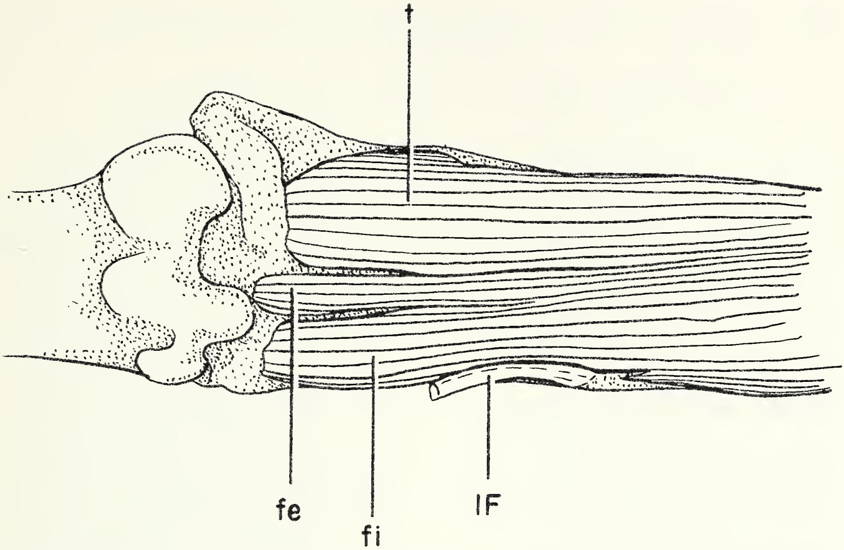

Fig. 7.—M. flexor digitorum longus in *Camptostoma obsoletum* CM 1390. See Fig. 1 for abbreviations.

femoral head. The head may be completely absent, or small and arising from the knee capsule rather than the femur itself (Fig. 7, and see Table 3). In *Myiodynastes bairdii* USNM 50913 it is miniscule, and slightly larger in *M. bairdii* LSU 100526.

The femoral head arises on the femoral shaft and is of moderate size in *Myiozetetes luteiventris* LSU 114492, *M. cayanensis* CM 1233, 1747, USNM 504542 and 504545, *M. similis* CM 927, USNM 504551 and 506248, *M. granadensis* LSU 31687, *Conopias trivirgata* YPM 2639 and 2640, *Myiodynastes luteiventris* AMNH 6696, CM 3979 and 4228, *Legatus leucophaius* USNM 510867, *Empidonomus varius* FMNH 288494 and 288498, *E. aurantioatrocristatus* AMNH 2462, *Elaenia flavogaster, Phaeomyias murina, Fluvicola pica,* and *Machetornis rixosus.*

The femoral head is large in *Pitangus lictor* AMNH 8528, *P. sulphuratus* CM 928, 3793, 3846, 4094, and 4224, *Myiozetetes similis* CM 3847, 3848, 3857, 4119, 4120, 4301, 4302, 4475, *Conopias inornatus* CM 541, *Conopias parva* CM 1784, *Empidonomus varius* FMNH 288497, *Tyrannus niveigularis* LSU 100525, *T. vociferans* USNM 87297 and 87298, *T. dominicensis* USNM 504541, *T. verticalis* CM 2871, 2872, 3360, 3361, 3362, 3367, 3368, 3370, 3371, 3372, 3373, 3374, and 3375, *T. forficatus* CM 3070 and 3085, *T. savana* CM

Table 3.—*Variations in Mm. flexor digitorum longus and flexor hallucis brevis in Tyrannidae.*[1]

	FDL			
Specimen	Fem. hd.	Fem. hd. tiny	Fem. hd. mod.–lrge.	FHB notched
Pitangus lictor AMNH 8528	+	–	+	–
Pitangus sulphuratus CM 928	+	–	+	+
Pitangus sulphuratus CM 3793	+	–	+	+
Pitangus sulphuratus CM 3846	+	–	+	–
Pitangus sulphuratus CM 4094	+	–	+	–
Pitangus sulphuratus CM 4224	+	–	+	+
Pitangus sulphuratus LSU 31688	/	/	/	/
Pitangus sulphuratus LSU 31689	/	/	/	/
Megarynchus pitangua CM 529	+	+	–	+
Megarynchus pitangua KU 56828	+	+	–	+
Myiozetetes luteiventris LSU 114492	+	–	+	+
Myiozetetes cayanensis CM 1233	+	–	+	+
Myiozetetes cayanensis CM 1747	+	–	+	–
Myiozetetes cayanensis USNM 504542	+	–	+	–
Myiozetetes cayanensis USNM 504545	+	–	+	+
Myiozetetes similis CM 921	+	–	+	+
Myiozetetes similis CM 927	+	–	+	+
Myiozetetes similis CM 3847	+	–	+	+
Myiozetetes similis CM 3848	+	–	+	–
Myiozetetes similis CM 3857	+	–	+	–
Myiozetetes similis CM 4119	+	–	+	+
Myiozetetes similis CM 4120	+	–	+	+
Myiozetetes similis CM 4301	+	–	+	+
Myiozetetes similis CM 4302	+	–	+	+
Myiozetetes similis CM 4475	+	–	+	+
Myiozetetes similis LSU 31686	/	/	/	/
Myiozetetes similis LSU 63738	/	/	/	/
Myiozetetes similis LSU 114491	/	/	/	/
Myiozetetes similis USNM 504551	+	–	+	–
Myiozetetes similis USNM 506248	+	–	+	–
Myiozetetes granadensis LSU 31687	+	–	+	+
Conopias inornatus CM 541	+	–	+	–
Conopias parva CM 1784	+	–	+	+
Conopias trivirgata YPM 2639	+	–	+	–
Conopias trivirgata YPM 2640	+	–	+	–
Myiodynastes luteiventris AMNH 6696	+	–	+	–
Myiodynastes luteiventris CM 3979	+	–	+	+
Myiodynastes luteiventris CM 4191	+	+	–	–
Myiodynastes luteiventris CM 4228	+	–	+	+
Myiodynastes bairdii LSU 100526	+	+	–	–
Myiodynastes bairdii USNM 50913	+	+	–	–
Myiodynastes maculatus CM 363	+	+	–	+
Myiodynastes maculatus CM 1402	+	+	–	+
Myiodynastes maculatus CM 4452	+	+	–	+
Myiodynastes maculatus LSU 108693	+	+	–	/

Table 3.—*Continued.*

Specimen	FDL			
	Fem. hd.	Fem. hd. tiny	Fem. hd. mod.–lrge.	FHB notched
Myiodynastes maculatus LSU 111091	+	+	–	/
Legatus leucophaius USNM 510867	+	–	+	+
Empidonomus varius FMNH 288494	+	–	+	+ L
Empidonomus varius FMNH 288497	+	–	+	+
Empidonomus varius FMNH 288498	+	–	+	+
Empidonomus aurantioatrocristatus AMNH 2462	+	–	+	–
Tyrannus niveigularis LSU 100525	+	–	+	+
Tyrannus melancholicus AMNH 6697	+	–	+	/
Tyrannus melancholicus CM 345	+	–	+	+
Tyrannus melancholicus CM 1054	+	–	+	+
Tyrannus melancholicus CM 1071	+	–	+	+
Tyrannus melancholicus CM 1785	+	–	+	+
Tyrannus melancholicus USNM 504538	+	–	+	–
Tyrannus melancholicus USNM 504539	+	–	+	+
Tyrannus vociferans USNM 87297	+	–	+	/
Tyrannus vociferans USNM 87298	+	–	+	–
Tyrannus crassirostris KU 42008	+	–	+	+
Tyrannus verticalis CM 2871	+	–	+	+
Tyrannus verticalis CM 2872	+	–	+	–
Tyrannus verticalis CM 3360	+	–	+	+
Tyrannus verticalis CM 3361	+	–	+	–
Tyrannus verticalis CM 3362	+	–	+	–
Tyrannus verticalis CM 3367	+	–	+	+
Tyrannus verticalis CM 3368	+	–	+	–
Tyrannus verticalis CM 3369	+	–	+	–
Tyrannus verticalis CM 3370	+	–	+	–
Tyrannus verticalis CM 3371	+	–	+	–
Tyrannus verticalis CM 3372	+	–	+	–
Tyrannus verticalis CM 3373	+	–	+	–
Tyrannus verticalis CM 3374	+	–	+	–
Tyrannus verticalis CM 3375	+	–	+	–
Tyrannus forficatus CM 2232	+	–	+	+
Tyrannus forficatus CM 3070	+	–	+	+
Tyrannus forficatus CM 3085	+	–	+	+
Tyrannus savana CM 1284	+	–	+	+
Tyrannus savana CM 3761	+	–	+	–
Tyrannus savana CM 3768	+	–	+	–
Tyrannus tyrannus CM 2446	+	–	+	+
Tyrannus tyrannus CM 2567	+	–	+	+
Tyrannus tyrannus CM 2863	+	–	+	+
Tyrannus dominicensis USNM 504541	+	–	+	–
Tyrannus caudifasciatus USNM 291915	–	–	–	+
Camptostoma obsoletum CM 1390	+	+	–	–
Elaenia flavogaster CM 1746	+	–	+	–
Mionectes oleagineus CM 1317	–	–	–	–

Table 3.—*Continued.*

	FDL			
Specimen	Fem. hd.	Fem. hd. tiny	Fem. hd. mod.–lrge.	FHB notched
Phaeomyias murina CM 1787	+	−	+	−
Lophotriccus galeatus CM 1294	−	−	−	+
Todirostrum cinereum CM 1876	−	−	−	−
Tolmomyias sulphurescens CM 1136	−	−	−	−
Platyrinchus coronatus CM 1866	−	−	−	−
Contopus virens CM 2858	+	+	−	+
Contopus virens CM 3069	+	+	−	+
Empidonax virescens CM 2013	+	+	−	+
Sayornis phoebe CM 2539	+	+	−	−
Sayornis phoebe CM 2773	+	+	−	−
Sayornis phoebe KU 046413	/	/	/	/
Pyrocephalus rubinus CM 1099	+	+	−	−
Fluvicola pica CM 1285	+	−	+	−
Machetornis rixosus CM 528	+	−	+	−
Attila spadiceus CM 1073	+	+	−	+
Myiarchus crinitus CM 2574	+	−	+	−
Myiarchus crinitus CM 2861	+	−	+	+

[1] Abbreviations: FDL, M. flexor digitorum longus; fem. hd., femoral head; mod.–lrge., moderate to large; FHB, M. flexor hallucis brevis; + and −, presence and absence; L & R, left & right; /, data not taken. See text for further explanation.

1284, 3761, and 3768, *T. tyrannus* CM 2446, 2567, and 2863, *T. crassirostirs* KU 42008, and *Myiarchus crinitus* CM 2574 and 2861.

The variation is summarized in Table 3.

M. extensor hallucis longus (Fig. 8:EHL) is a narrow, bipennate muscle arising fleshy on the craniomedial surface of the medial cotyla of the tarsometatarsus just distal to the proximal articular surface of the tarsometatarsus. It also has a fleshy origin from the Tuberositas M. tibialis cranialis just distal to the insertion of M. tibialis cranialis. The fibers of this origin join those of the rest of the muscle (parallel-fibered at this point) at a highly acute angle. The belly extends nearly the length of the tarsometatarsus, passing medial to the tendons of M. extensor digitorum longus, narrows to a tendon which passes underneath a ligament at the base of the proximal phalanx of the hallux, and thence to the dorsal surface of the hallux. It inserts at the base of the ungual phalanx.

The belly extends only about three-fourths the length of the tarsometatarsus in *Legatus leucophaius* USNM 510867 and *Empidonomus aurantioatrocristatus* AMNH 2462, two-thirds in *Myiozetetes cayanensis* CM 1747.

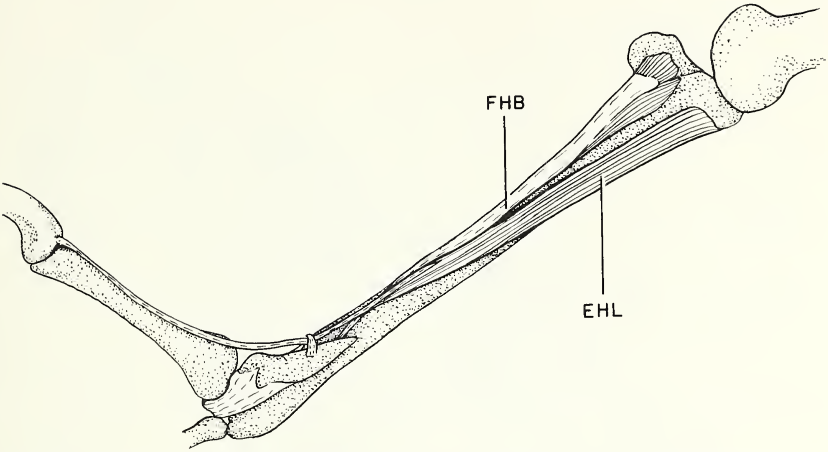

Fig. 8.—Intrinsic muscles of the pes in *Tyrannus melancholicus* CM 1785. See Fig. 1 for abbreviations.

The other species examined are as described for *Tyrannus melancholicus.*

M. flexor hallucis brevis (Fig. 8:FHB) is a small muscle lying on the medial surface of the tarsometatarsus. The caudal fibers arise fleshy on the medial and caudomedial surface of the hypotarsus and the medial parahypotarsal fossa, the cranial fibers from the caudal surface of the head of the medial hypotarsal ridge of the tarsometatarsus. The belly is asymmetrically bipennate. There is a gap between the caudal and the cranial fibers proximally giving the muscle a notched appearance in *T. melancholicus* CM 1071, 1054, and 1785; it is slightly notched in USNM 504539. The belly extends about half way down the tarsometatarsus and gives way to the tendon of insertion. The tendon passes lateral to Metatarsal I and inserts on a large fibrous pad (the articular cartilage), which in turn inserts on the base of the proximal phalanx of the hallux.

M. flexor hallucis brevis varies in whether or not a notch is present. This variation is summarized in Table 3.

There is some variation in the length of the belly; it extends one-third rather than one-half way down the tarsometatarsus in *Pitangus lictor* AMNH 8528, *P. sulphuratus* CM 3846 and 4094 (half way in 3793 and 4224), *Myiozetetes luteiventris* LSU 114492, *M. similis* CM 3847, 4120, 4302 (half way in 3848 and 4119), *Myiodynastes luteiventris* CM 3979, 4191 and 4228, *M. maculatus* 4452, *Tyrannus niveigularis* LSU 100525, *T. verticalis* CM 2871, 3360, 3362, 3368, 3371,

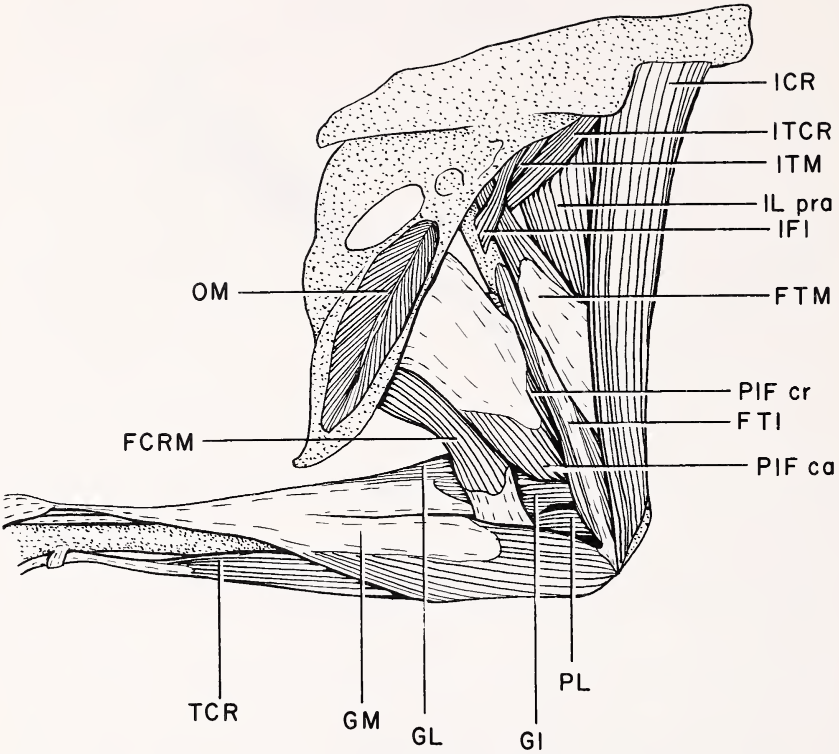

Fig. 9.—Superficial muscles of the medial surface of the thigh and crus in *Tyrannus melancholicus* AMNH 6697. See Fig. 1 for abbreviations.

and 3374 (but half way in CM 2872, 3361, 3370, 3372, 3373, and 3375), *T. savana* CM 3761 and 3768, and *T. tyrannus,* and three-fourths to seven-eighths the way down in *Myiozetetes similis* 4301 and 4475 and *T. crassirostris.*

M. abductor digiti IV is a tiny, roughly strap-shaped muscle arising fleshy on the lateral surface of the distal end of the tarsometatarsus, and extending less than one-fourth the length of that bone. Its tendon of insertion merges with the joint capsule at the base of digit IV.

The other species examined are as above.

M. lumbricalis is absent in all the species examined.

DISCUSSION

Few hindlimb muscles vary qualitatively among the species of Tyrannidae examined. Those that do will be discussed individually below,

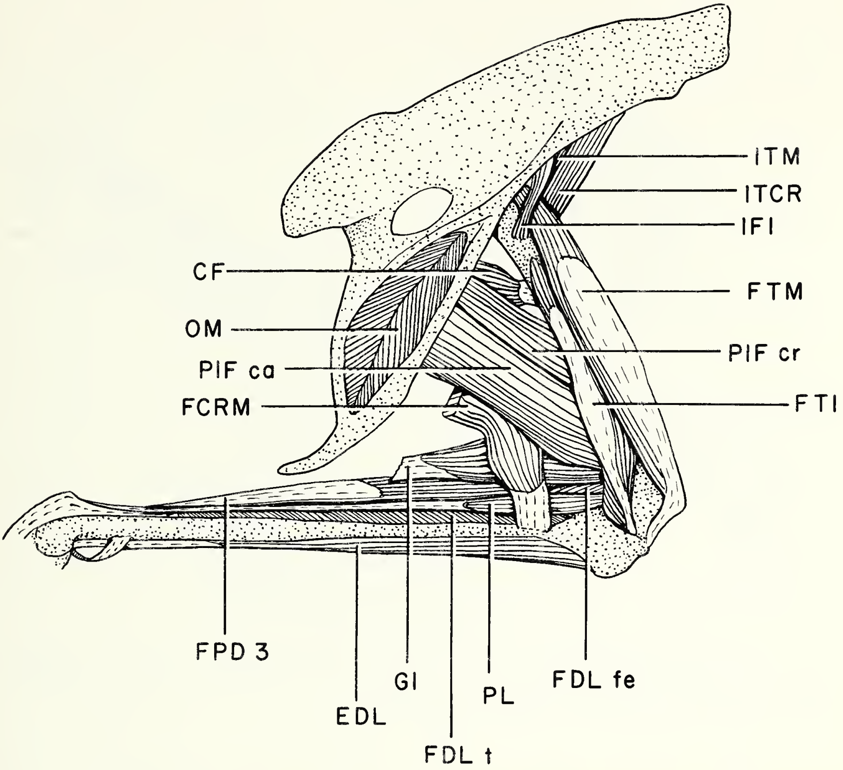

Fig. 10.—Second layer of muscles of the medial surface of the thigh and crus in *Tyrannus verticalis* CM 3360. See Fig. 1 for abbreviations.

with reference both to variation in other passerines and to potential usefulness in formulating phylogenetic hypotheses.

M. iliotibialis lateralis.—The postacetabular portion (IL pa) of this muscle is present in most oscines, including *Menura* and *Atrichornis* (Raikow, in press), *Paradisaea rubra* (Berger, 1956), 10 genera of Laniidae (Raikow et al., 1980), *Fregilupus varius* (Berger, 1957), numerous New World nine-primaried oscines (Stallcup, 1954; Raikow, 1978), 29 species of Estrildidae and 18 species of Ploceidae (Bentz, 1979), and representatives of numerous other passerine families (Hudson, 1937). The Old World suboscines have the pre- and postacetabular portions, but have lost the acetabular portion, leaving a gap between the two (except in the Acanthisittidae in which the muscle is unreduced [Raikow, manuscript]). It appears that the only species in which IL pa

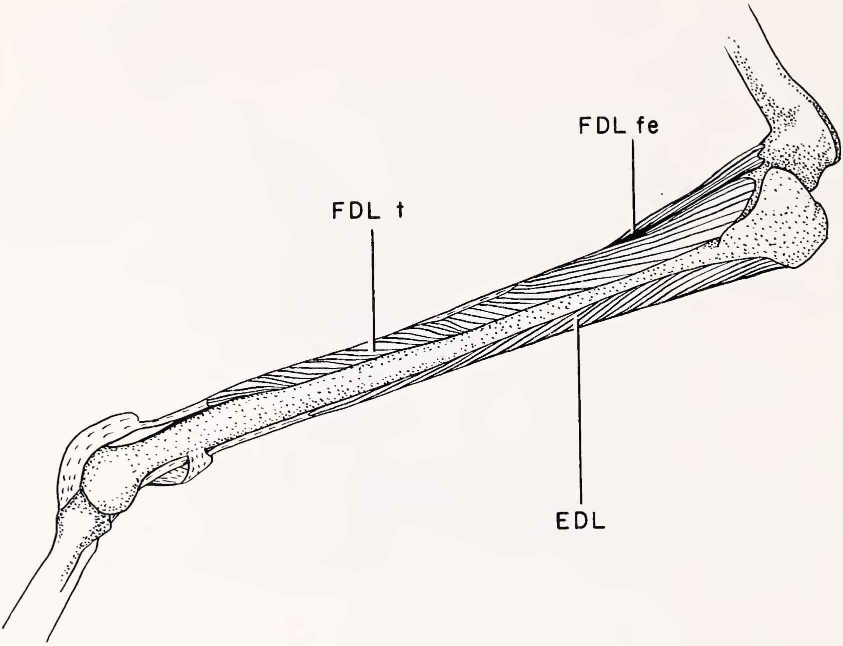

Fig. 11.—Deep layer of muscles of the medial surface of the crus in *Tyrannus melancholicus* CM 1785. See Fig. 1 for abbreviations.

has been reported absent are *Sayornis phoebe, Empidonax virescens, Myiarchus crinitus,* and *Tyrannus tyrannus* (Tyrannidae), *Stelgidopteryx ruficollis,* and *Petrochelidon albifrons* [=*Hirundo pyrrhonota*] (Hirundinidae) (Hudson, 1937), and *Procnias nudicollis* (Cotingidae) (George and Berger, 1966:387). Raikow (unpublished observation) found IL pa lacking in *Pipra erythrocephala* (Pipridae) as well.

The above comparison with passerines outside of the monophyletic Tyrannidae indicates that reduction of M. iliotibialis lateralis is a derived condition. It appears to have occurred several times within suboscines, and the distributional pattern of loss of IL pa in the Tyrannidae suggests that this loss is probably independent of other suboscines. In the Old World suboscines IL pa is much wider than in tyrannids, suggesting that further reduction is occurring within the latter group. However, in all of the kingbird species in which a postacetabular portion occurs, there are individuals that lack it. This irregularity suggests polymorphism or possibly the atavistic reappearance of a lost structure (Raikow, 1975; Raikow et al., 1979; Hall, 1984).

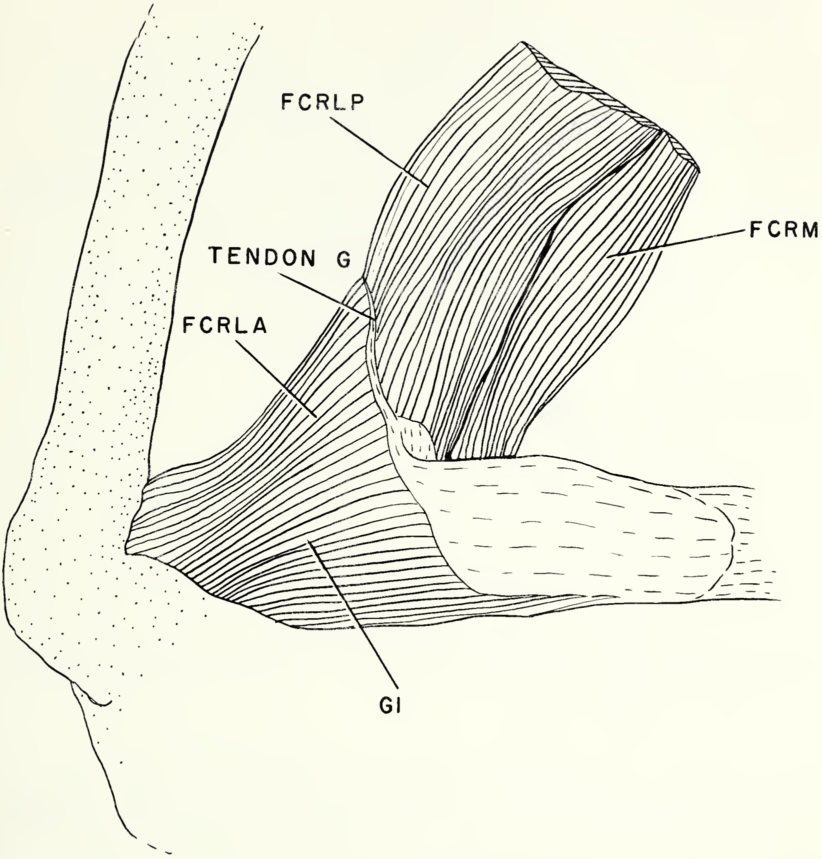

Fig. 12.—M. flexor cruris lateralis in *Machetornis rixosus* CM 528. See Fig. 1 for abbreviations.

It is possible that, with dissection of representatives of all tyrannid species, the level at which the reduction of M. iliotibialis lateralis is synapomorphous can be determined. Because some tyrannids possess the muscle in its primitive, unreduced state, reduction must be derived at some "lower" level, within the family. Large samples will be necessary to assess the frequency of reappearance of IL pa in species that have lost it altogether, such as some of the kingbirds and *Sayornis phoebe* (1 individual in 15 of the latter had IL pa, or 6%).

M. flexor cruris lateralis.—Hudson (1937) did not report any pe-

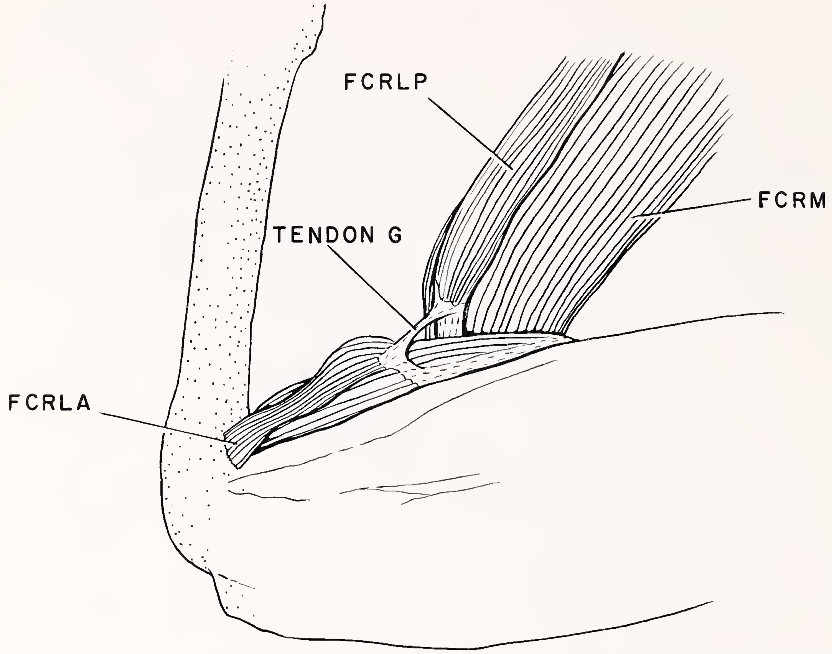

Fig. 13.—M. flexor cruris lateralis in *Sayornis phoebe* CM 2773. See Fig. 1 for abbreviations.

culiarity in M. flexor cruris lateralis for *Tyrannus tyrannus*. George and Berger (1966:400–404) reported variation in the extent of insertion of pars accessoria on the femur among species of nonpasserines. A. S. Gaunt (unpublished observation) noted that pars accessoria is "small and weak" in *Terpsiphone*, an Old World flycatcher (Monarchinae); pars accessoria is absent in the Hirundinidae (Gaunt, 1969). There is no published account of variation in the size of the muscle among closely related species, however, nor of individual variation. The extensive variation in this muscle in certain tyrannids has interesting evolutionary implications; these are discussed elsewhere (McKitrick, manuscript).

M. gastrocnemius.—Raikow (1978) reported variation in the presence of a superficial head and patellar band in M. gastrocnemius pars medialis. He found these features absent in icterids, most carduelines, and some cardinalines and thraupids, but considered that the use of this absence as a synapomorphy would conflict with other data. Most kingbirds lack the superficial head and patellar band, as do many non-

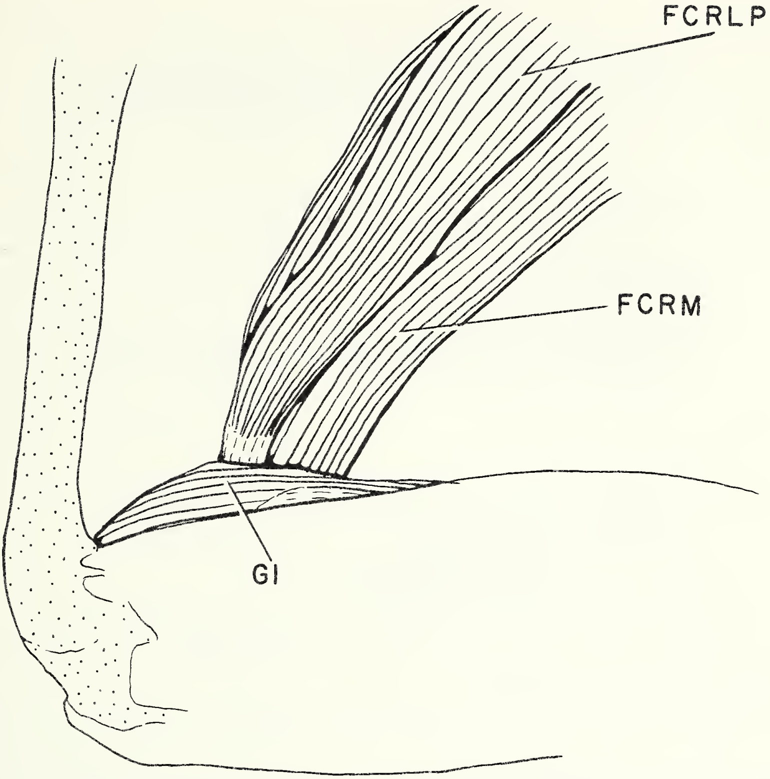

Fig. 14.—M. flexor cruris lateralis in *Contopus virens* CM 2858. See Fig. 1 for abbreviations.

kingbird tyrannids; it is not possible at this point to determine whether presence of these character states represents primitive retention or independent origin (or reappearance).

M. flexor perforatus digiti IV.—The occurrence of a distal head in this muscle is widespread in nonpasserines (Hudson, 1937; George and Berger, 1966; Berman and Raikow, 1982; Swierczewski and Raikow, 1981), but most oscines lack the distal head (Raikow, 1976, 1978). The presence of a second distal belly in the specimen of *Machetornis* is clearly derived (although it could be anomalous) as is the absence of a distal head in the specimen of *Conopias inornatus,* but these conditions are autapomorphies and can say nothing about phylogenetic relationships.

M. flexor hallucis longus.—In most passerines this muscle has three

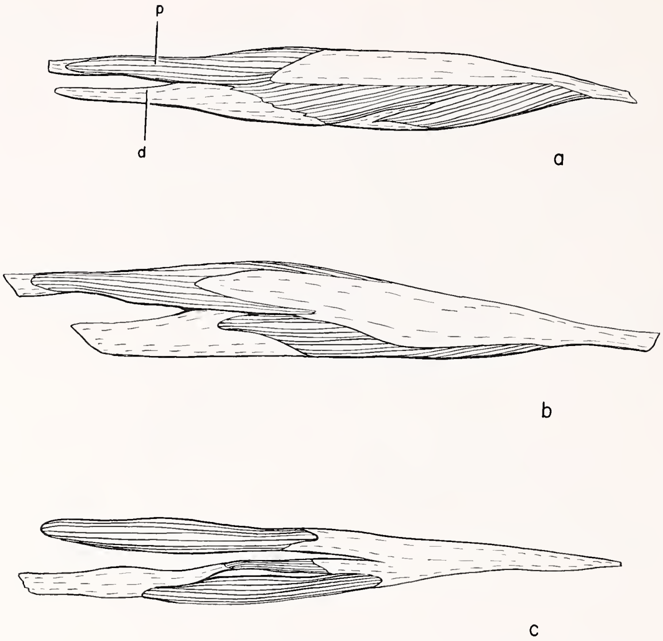

Fig. 15.—Variations in M. flexor perforatus digiti IV. d = distal head, p = proximal head. See text for discussion of variations.

heads, the intermediate head arising in common with the lateral head and passing medial to the tendon of insertion of M. iliofibularis (Raikow, 1976, 1978; Borecky, 1977; Bentz, 1979; Raikow et al., 1980). This is also the case in most of the tyrannids I have examined. In *Eurylaimus ochromalus* Raikow (manuscript) found two small intermediate heads, one arising with the lateral head and one with the medial head. He considered that this could be anomalous. The other Old World suboscines have the common passerine condition of a lateral origin for the intermediate head. Several derived conditions occur within the kingbird group that were absent in tyrannids outside that group. A medial origin of the intermediate head occurs in all specimens of *Myiozetetes similis* (15), all *M. cayanensis* (4), *M. luteiventris* (1), all *Conopias trivirgata* (2), the right leg of the one *C. parva,* five of seven *Pitangus sulphuratus, Legatus leucophaius* (1), one of three *Tyrannus savana,* the left leg of one of three *T. forficatus,* and 10 of 14 *T. verticalis* examined. The one *M. granadensis* lacks the intermediate head. In these three *Tyrannus* species the intermediate head is tiny, which may indicate incipient loss. Conceivably, the three *Tyrannus* species con-

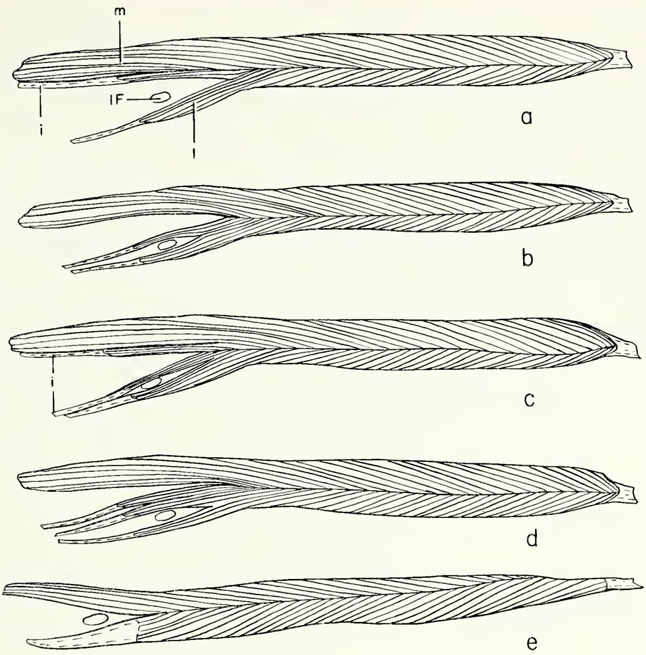

Fig. 16.—Variations in M. flexor hallucis longus. i = intermediate head(s), l = lateral head, m = medial head. IF = tendon of insertion of M. iliofibularis. See text for discussion of variations..

stitute a monophyletic group within the genus and the other species just mentioned are another monophyletic group, but the irregularities in distribution of these derived characters preclude strong hypotheses.

M. flexor digitorum longus.—Hudson (1937:47) described *Tyrannus tyrannus* as having two rather than three heads of origin for this muscle, but he evidently considered the tibial and fibular heads as one, the femoral being the second. The muscle has a femoral head in *Corvus* (Hudson, 1937) and *Paradisaea rubra* (Berger, 1956). In the many New World nine-primaried oscines examined by Raikow (1978) only *Sericossypha* had a femoral head, but estrildids and ploceids do not (Bentz, 1979), nor do the Old World suboscines (Raikow, manuscript). Raikow (unpublished observation) found a small "femoral" head arising on the joint capsule in *Procnias nudicollis* (Cotingidae) and *Certhiaxis cinnamomea* (Furnariidae), and a well developed femoral head in *Dendrocolaptes certhia.* Most species in the kingbird group have a well developed femoral head, with the exception of *Megarynchus pitangua,* *Myiodynastes maculatus,* and *M. bairdii* in which it is very small and arises on the joint capsule, and *Tyrannus caudifasciatus,* in which it is absent. One specimen of *Myiodynastes luteiventris* (CM 4191) had a small femoral head, but three other specimens did not. Absence of a femoral head or presence of a small one occurs in members of the subfamilies Elaeniinae and Fluvicolinae of the Tyrannidae (as recognized by Traylor [1979]), and a moderately well developed femoral head also occurs in the Elaeniinae, as well as in the *Myiarchus* group (sensu Traylor, 1977) and the kingbird group. This suggests that development of this feature may have occurred several times within the Tyrannidae. It is possible that the kingbirds exclusive of *Megarynchus* and *Myiodynastes* form a clade; this would require *Tyrannus caudifasciatus* to have lost the femoral head secondarily (unless the one specimen examined is atypical); it would also indicate that *Myiodynastes luteiventris* is independently acquiring a true femoral head. Such multiple instances of origin and loss are entirely possible, especially in light of the irregular patterns of variation in other hindlimb muscles in the Tyrannidae.

M. lumbricalis.—This muscle is present in many oscines (Stallcup, 1954; Raikow, 1978) and in Old World suboscines (Raikow, manuscript). Its absence in the tyrannids examined suggests its possible loss at some point within the New World suboscines, but at what point remains to be determined.

The results of this study show that, while most hindlimb muscles are uniform in the Tyrannidae, certain muscles are extremely variable within kingbird species, the group that is examined most intensively herein. This is the first study of avian hindlimb muscles to address this potential problem, and it shows that phylogenetic hypotheses based on muscle data are highly risky for the kingbirds and possibly for the Tyrannidae as a whole. The question naturally arises, what significance do these results have for other phylogenetic studies of birds based on hindlimb muscles? Are the results of such studies invalid? Phylogenetic studies based on comprehensive myological comparisons and cladistic analysis indicate that they are not. The irregular occurrence of primitive and derived character states in the kingbird group defy perception of a clear phylogenetic pattern. Other studies have evidently not experienced such difficulties, and while there are always character conflicts, a coherent phylogenetic picture usually emerges. The results of one such study of the Piciformes, by Swierczewski and Raikow (1981), are supported by the similar phylogenetic hypotheses of Simpson and Cracraft (1981) based on osteology; a myological study of relationships among the Old World suboscines (Raikow, manuscript) corroborates the work of Sibley et al. (1982) using DNA hybridization. It should be pointed out, however, that these studies dealt with relationships at a higher taxonomic level than the present one, and therefore may not be strictly comparable.

The results of the present work on Tyrannidae, especially kingbirds, hint that multiple origin and loss may have been extensive in the evolutionary history of this group, possibly associated with its expansion into virtually all of the diverse habitats of Central and South America (Traylor and Fitzpatrick, 1982). I believe that dissection of very large series of individuals of a variety of tyrannid species, especially those in which variation is now known to be irregular, could elucidate this idea. Assessing the frequency of occurrence of primitive and derived states within species would help to determine whether these are "normal" for the species, or whether some represent atavisms or polymorphisms. The latter may indicate a transient phase of evolutionary change and the possibility that parallel change is occurring in a number of species simultaneously (see McKitrick, manuscript).

CONCLUSIONS

The myological synapomorphies postulated by Raikow (1982) for the Passeriformes are corroborated for the Tyrannidae by the present study. However, the assumption that individual variation in hindlimb muscles is insignificant is invalid for the Tyrannidae, although it may be correct for other groups. The pattern of variation in certain species in this family suggests the possibility of a mode of evolution, involving frequent parallel changes in musculature, that may be atypical among birds. It is possible, however, that such variation is a normal part of evolutionary change; dissection of larger series of specimens of non-tyrannid species will be necessary to investigate this.

ACKNOWLEDGMENTS

I thank the members of my doctoral committee at the University of Pittsburgh for advice and support throughout this study and for criticising an earlier draft of this paper: Melvin Kreithen, Kenneth Parkes, Jeffrey Schwartz, William Searcy, and, especially, Robert Raikow. I thank the following for the loan of specimens: George Barrowclough and Wesley Lanyon (American Museum of Natural History), Kenneth Parkes, D. Scott Wood, and James Loughlin (Carnegie Museum of Natural History), John Fitzpatrick (Field Museum of Natural History), Marion Mengel (University of Kansas), James V. Remsen, Jr. (Louisiana State University), Richard Zusi (National Museum of Natural History), Charles Sibley, and Eleanor Stickney (Peabody Museum of Natural History). John Anderton prepared the illustrations. I am especially grateful to K. Parkes, D. S. Wood, and J. Loughlin for help in innumerable ways. This material is based upon work supported by the National Science Foundation under grants DEB-8010898 and BSR-8314729 to R. Raikow.

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SYSTEMATICS AND PALEOECOLOGY OF MALACOSTRACAN ARTHROPODS IN THE BEAR GULCH LIMESTONE (NAMURIAN) OF CENTRAL MONTANA

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Abstract

The limestones of the Bear Gulch Member of the Heath Formation (Namurian, Mississippian) have become famous for the quality of their diverse vertebrate and invertebrate faunas, including numerous specimens of malacostracous arthropods. The malacostracan elements of the fauna include *Dithyrocaris rolfei, Sairocaris centurion, Perimecturus rapax, Tyrannophontes theridion, Aenigmacaris cornigerum, Crangopsis eskdalensis,* and *Belotelson magister.* These taxa have been redescribed using known, but previously unstudied material analyzed by standard and ultraviolet photographic techniques. Major systematic changes include rendering *Bairdops beargulchensis* the junior synonym of *Tryannophontes theridion,* and transfer of the Sairocarididae to the Archaeostraca, with the consequence that the order Hoplostraca is unnecessary. Interpretations concerning trophic positions and habitat preferences based on functional morphological analyses confirm the earlier observation (Schram, 1981) that the four basic feeding types of Paleozoic Crustacea are found in this locality—rapacious carnivores, scavengers, filter feeders, and algal-detrital feeders. Paleontological, sedimentological, and stratigraphic information from the limestones of the Bear Gulch Member are interpreted to represent carbonate deposition in a calm, shallow, tropical basin with a restricted, Mediterranean-type circulation pattern. The basin margins supported growth of algal and bacterial mats, which provided micritic material to the sediment of the basin center. The water column was well oxygenated and normal marine near the surface with higher salinity bottom waters overlying sediments with anaerobic pore spaces. Sedimentological and fossil evidence indicate a vital-pantostrate biocenosis (Schäfer, 1972).

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INTRODUCTION

The diverse fauna found in the limestones of the Bear Gulch Member of the Heath Formation in central Montana has received considerable attention since the early work of Melton (1971). The locality has become famous for the quality and diversity of its invertebrate and vertebrate fauna, which includes fish, shrimp, annelids, xiphosurans, conulariids, starfish, brachiopods, cephalopods, gastropods, bivalves, sponges, and numerous unidentified forms (Lund and Horner, 1979). Notable by their absence or rarity are corals, trilobites, stalked echinoderms, echinoids, and bryozoans.

Numerous papers describing fish morphology, taxonomy, and paleoecology have been based on Bear Gulch finds (Lund, 1974, 1977*a,* 1977*b,* 1980, 1982; Lund and Zangerl, 1974; Zidek, 1980). Work on the invertebrate portion of the fauna is being pursued at a slower pace. Sponges (Rigby, 1979), "worms" (Schram, 1979*d*), conodont-eating animals (Conway-Morris, 1979), and limulines (Schram, 1979*c*) have received some attention. The flora of the Bear Gulch Limestone Beds is currently being prepared for publication (R. Lund, personal communication, 1985).

The malacostracan crustaceans were described (Schram and Horner, 1978; Schram and Schram, 1979) on the basis of earlier finds. A few phyllocarid arthropods are currently under study (R. Lund, personal communication, 1985).

The ecology of the Bear Gulch malacostracan assemblage, as well as recently discovered fossil material, has been virtually unexplored. The purposes of this paper are: 1, to expand upon the published descriptions of the Bear Gulch malacostracans utilizing recently collected and previously described material; 2, to re-evaluate the taxonomic position of each member of the malacostracan assemblage based on material now available; and, 3, to ascertain some of the trophic relationships and habitat preferences of these malacostracans in their environment.

STRATIGRAPHY

The Bear Gulch Limestone Beds alternate with other limestones and black shales to form the Bear Gulch Member of the Heath Formation in the Big Snowy Group (Williams, 1981) (Fig. 1). The Bear Gulch Limestone was termed a lithographic limestone or *plattenkalke* by Williams (1981). Fossils of marine organisms with chitinous and phosphatic hard parts of excellent quality are found throughout the rhythmically alternating massive micrite and fine-grained, platy, shaly limestone beds (Williams, 1981).

The Big Snowy Group in central and eastern Montana and the correlative Big Snowy Formation of western Montana represent sediments

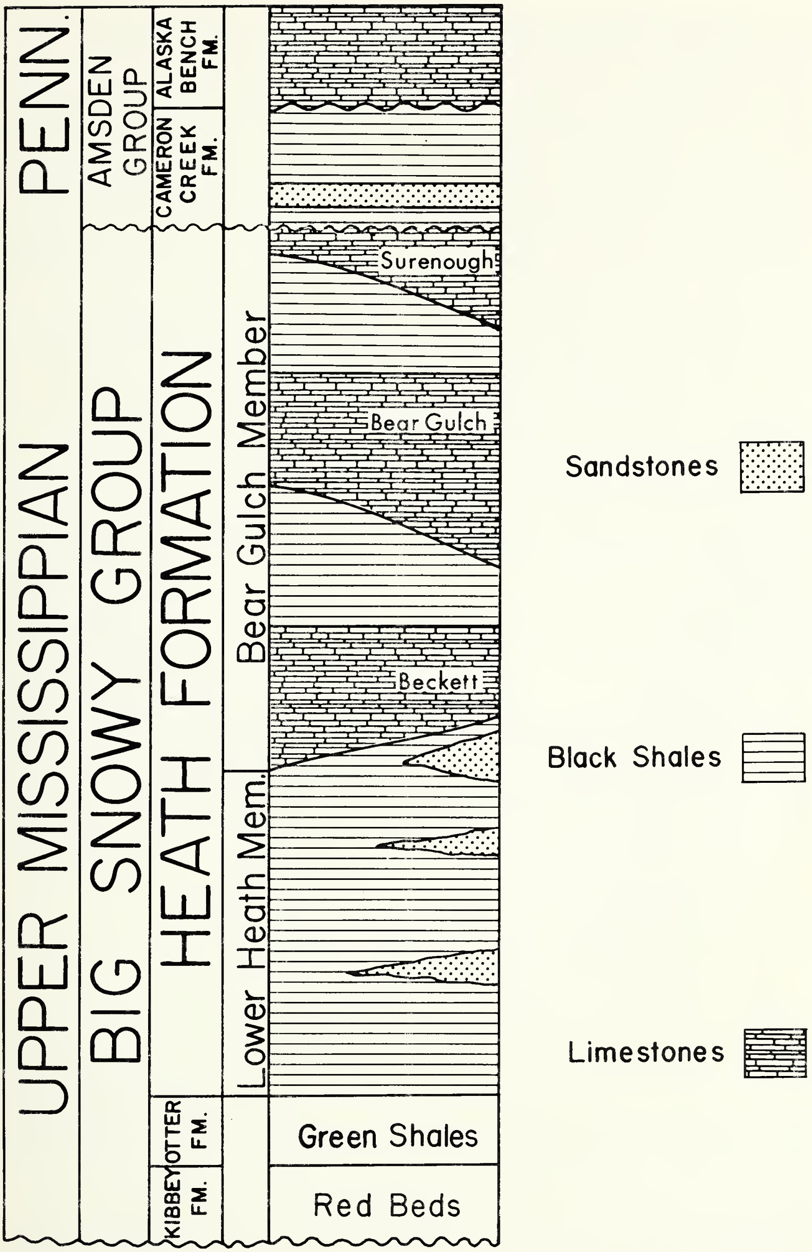


Fig. 1.—Generalized stratigraphic section of the mid-Carboniferous rocks in central Montana exposed on Potter Creek Dome. After Williams, 1981.

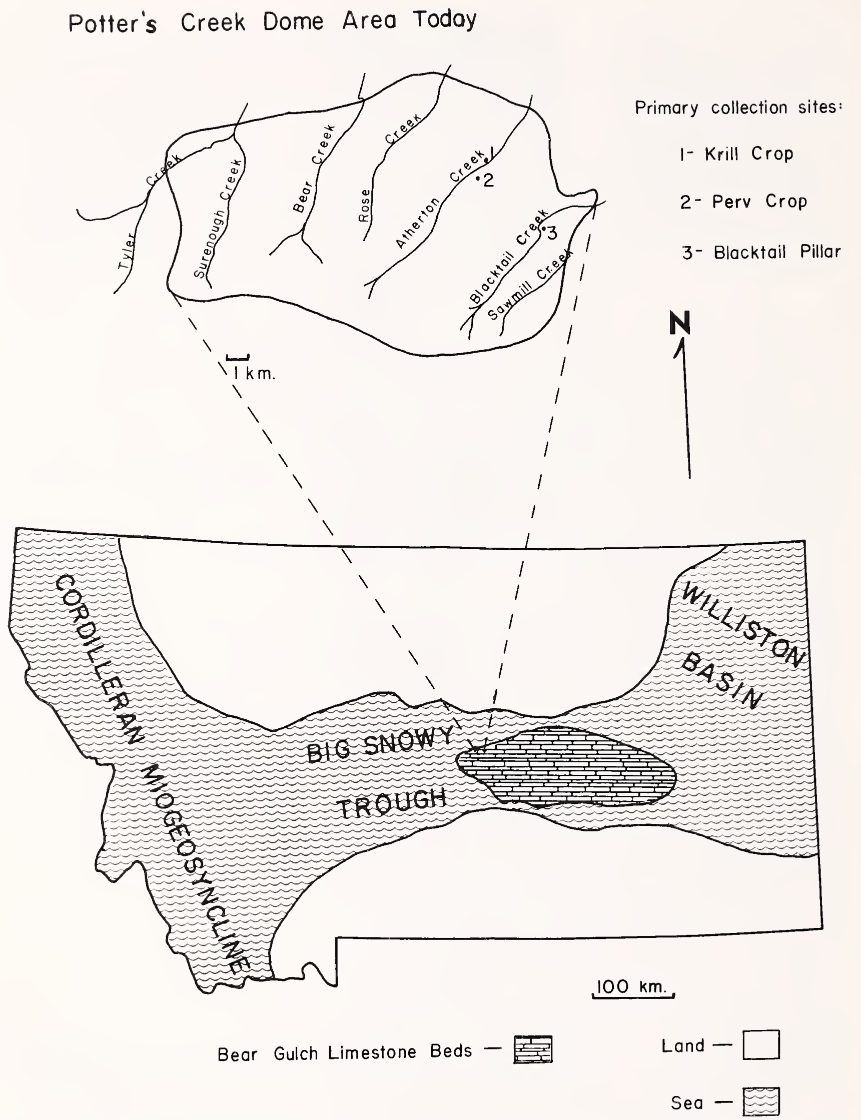


Fig. 2.—Relationship of Potter's Creek Dome and the Bear Gulch Limestone Beds to Late Mississippian paleogeography in Montana.

deposited in the Big Snowy Trough during the Late Mississippian (Maughan and Roberts, 1967; Williams, 1981). The Big Snowy Trough was a long, narrow, marine embayment at this time, connecting the Cordilleran miogeosyncline with the Williston Basin (see Fig. 2;

Maughan and Roberts, 1967; Sando et al., 1975; Williams, 1981). The entire unit represents an unconformity-bounded, transgressive sequence overlying the Lower Mississippian Madison Group and underlying the Lower Pennsylvanian Amsden Group (Smith and Gilmour, 1979). The Big Snowy Group in central Montana is made up of three diachronous units, older in southwestern Montana, younger in the Big Snowy Trough, and youngest in the Williston Basin of eastern Montana, the Dakotas, and southern Canada (Sando, 1976). The Kibbey Formation at the base of the transgression represents sediments deposited at the margin of the transgressing sea. The Otter Formation was deposited offshore from the Kibbey and is comprised of shales and limestones. The Heath Formation is composed of black shale and limestone that accumulated along the axis of the Big Snowy Trough (Sando et al., 1975). The Bear Gulch Limestone Beds and laterally correlative black shale make up the Bear Gulch Member of the Heath Formation. The age and stratigraphic relationships of the Bear Gulch Limestone Beds are controversial. Some authors have assigned the Bear Gulch Limestone Beds to the overlying Amsden Group (see Maughan, 1984). Based on evidence from cephalopods (Saunders, 1973), conodonts (Scott, 1973), and palynomorphs (Cox, written communication to R. Lund, 1982 and 1984) a Namurian, Late Mississippian age seems to be the most reliable determination. The stratigraphy of Williams (1981) has been accepted for this paper.

Bear Gulch Limestone crops out only on Potter's Creek Dome. This small dome (350 km^2) is located approximately 50 km southeast of Lewistown in Fergus County, Montana, and about 30 km northeast of the Big Snowy Mountains. The Bear Gulch Member covers some 5000 km^2, mostly in the subsurface, from T36E to T21E and from R16N to R8N (Williams, 1981) (Fig. 2).

The carbonate rocks of the Bear Gulch Member of the Heath Formation vary in thickness depending on their position relative to the depocenter of the basin. Near the depocenter, in the Atherton Creek area, the unit is about 30 m thick. Westward, in the region of Tyler Creek, the unit thins to 2 m or less. The Bear Gulch Member is composed of three carbonate lenses interbedded with, and separated vertically by, black shale. Each lens has been interpreted to represent a small, en echelon-fault-formed basin around the margins of which algae and bacteria precipitated the micrite by which the basins were eventually filled (Williams, 1981). It is in this setting that the Bear Gulch fauna, including the malacostracans, has been preserved.

MATERIALS

Specimens used in this study were collected over fifteen field seasons from 1969 to 1983. Collections were made by quarrying suitable accessible pillars of Bear Gulch Member limestone on Potter's Creek Dome.

Specimens utilized in this study are deposited in the museum collections at the Carnegie Museum of Natural History, the Museum of Paleontology at the University of Montana in Missoula, the San Diego Museum of Natural History, and the Field Museum of Natural History. Several hundred pertinent specimens from the Carnegie Museum of Natural History and the University of Montana were examined. Twenty-eight specimens from the Carnegie Museum of Natural History (CM) and 21 from the University of Montana (UM) were borrowed for detailed study. Additionally, 17 specimens were provided to the authors by Frederick Schram, San Diego Museum of Natural History. Included in the specimens from the University of Montana are the holotypes of *Aenigmacaris cornigerum, Bairdops beargulchensis, Dithyrocaris rolfei, Perimecturus rapax,* and *Sairocaris centurion.* Seven specimens of *Tyrannophontes theridion,* were borrowed from the Field Museum (FMNH) in Chicago for comparison to Bear Gulch material.

SYSTEMATIC PALEONTOLOGY

Class Malacostraca Latreille, 1802
Subclass Phyllocarida Packard, 1879
Order Archaeostraca Claus, 1888
Suborder Rhinocarina Clark *in* Zittel, 1900
Family Rhinocarididae Hall and Clark, 1888
Genus ***Dithyrocaris*** Scouler, 1843
Dithyrocaris rolfei Schram and Horner, 1978
Fig. 3

Diagnosis.—A large rhinocarid up to 10 cm in length; median dorsal plate elongate and narrow; carapace covered with papillae; fine setae ornament posterior half of ventral carapace margin; telson with dorsal carina, shorter than furcal rami.

Description.—Carapace suboval, covering entire cephalothorax and four abdominal segments. Antero-dorsal granules, anterior tubercles, cephalic, nuchal, and mesolateral carinae prominent (UM5193, CM34443, CM34444) (Fig. 3). Medial dorsal plate elongate, very narrow, extending from posterior terminus of rostral plate to near posterior margin of carapace, separated from carapace by distinct marginal groove, terminates as mid-dorsal spine extending beyond posterior carapace margin. Entire surface of carapace ornamented by posteriorly directed papillae, most dense dorsal to the mesolateral carinae and becoming less dense or absent laterally. Perimeter of carapace bordered by broad doublure; postero-lateral margin with posteriorly directed setae (CM34444). Postero-ventral spines prominent; about one-half the length of an abdominal segment.

Seven abdominal segments present. Four weakly sclerotized segments covered by carapace; outlined by longitudinal and transverse sclerotized ridges beneath carapace. Eight transverse mid-dorsal bands visible under carapace, decreasing in length anteriorly, represent boundaries of thoracic somites. Four sclerotized abdominal somites protrude beyond carapace valves, ornamented by postero-ventrally directed striae, producing a crude chevron pattern symmetrical about mid-dorsal line. Postero-ventral corners of poorly developed pleurae marked by spines (CM34444).

Telson narrowly triangular in plan view, with prominent medial carina and weak marginal ridges (CM34443). Styliform furcae with longitudinal carina along proximal margin; single row of closely spaced setal (?) pits border proximal, ventral surface of furcae; slightly longer than telson.

Appendages unknown.

Materials and measurements.—Measurements, in centimeters, of all *Dithyrocaris rolfei* specimens used in this study are given in Table 1.

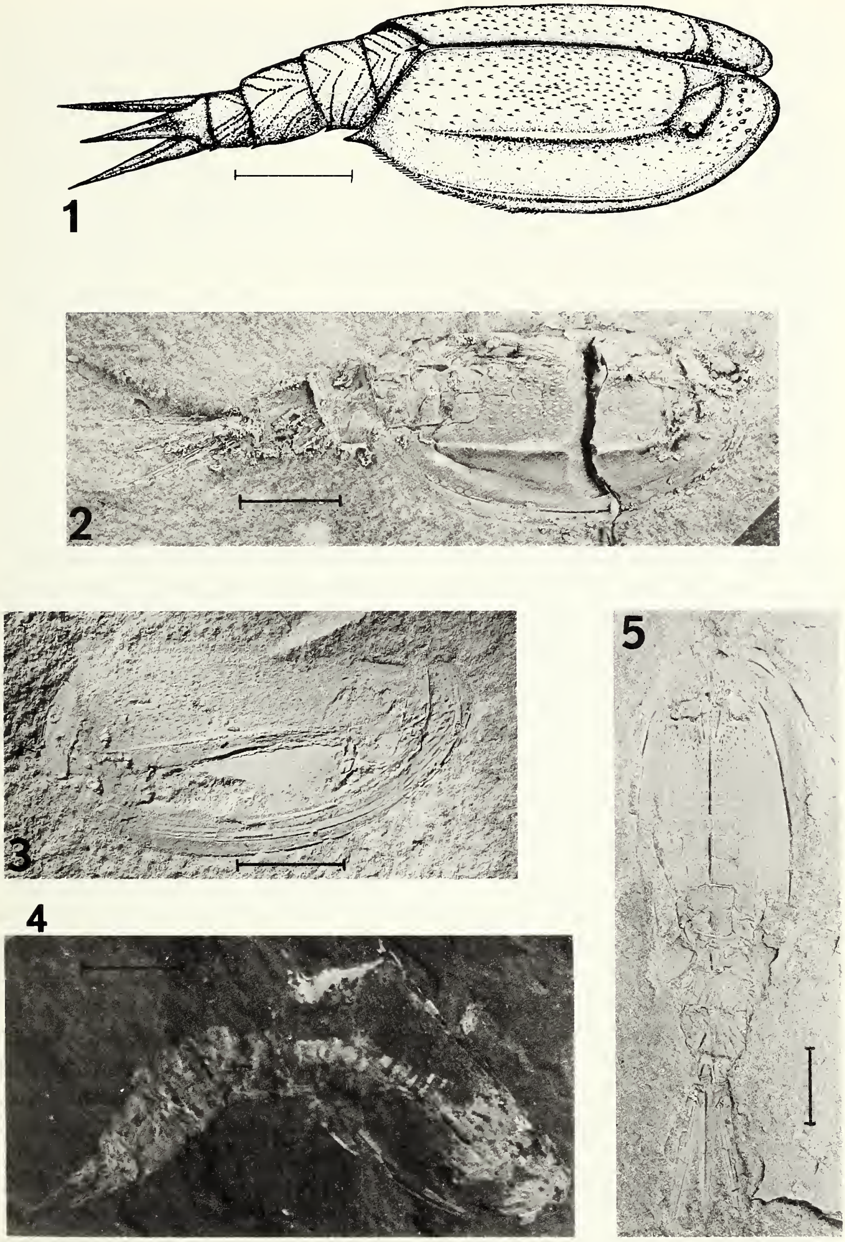


Fig. 3.—*Dithyrocaris rolfei* Schram and Horner. 3.1, lateral reconstruction. 3.2, CM34444. 3.3, UM5193 carapace, right valve, lateral view. 3.4, UM6225, holotype, ultraviolet photographic technique. 3.5, CM34443. Bars represent 1 cm.

Table 1.—*Representative measurements of* Dithyrocaris rolfei *(in cm).*

Catalog no.	Carapace midline	Abdominal segments							Telson	Caudal furca
		a_1	a_2	a_3	a_4	a_5	a_6	a_7		
UM5193	3.55									
*UM6225	3.13†	.33	.26				.59	.73	1.24	1.40
CM34445	3.03	.36	.32	.33	.33	.39	.47	.69		
CM34444	3.35	.28	.33	.30	.35		.45	.67	1.28	1.70
CM34443	4.50	.35	.41	.27	.42	.47	.56	.82	1.74	1.91
†UM6180	2.90								1.03	1.30
†UM6199									1.60	1.87
†UM6250									1.40	1.70
UM6257	3.10									
†FMNH32086	5.20									
†FMNH32087	2.63									

† From Schram and Horner, 1978.
* Holotype.

Remarks.—*Dithyrocaris rolfei* is sometimes well preserved as entire mineralized specimens or impressions in micrite and shaly limestone. This quality of preservation makes possible comparison to two other species in the genus, *Dithyrocaris testudinea* (Scouler, 1835), and *D. paradoxoides* (de Koninck, 1844), which are also described from whole animal fossils. The surface ornamentation of the carapace on each of the species is so distinctly different that identification can be made on this basis alone. The carapace of *D. testudinea* is covered by swirling, posteriorly directed terrace lines. That of *D. paradoxoides,* as reconstructed by Rolfe (1969), has a largely smooth unornamented carapace surface. The overall setose nature of *D. rolfei* is distinctly different from either of these. Like *D. rolfei, D. testudinea* has a small postero-ventral spine and no carapace horn. *Dithyrocaris paradoxoides* has large postero-ventral spines, a distinct carapace horn and, like *D. rolfei,* a telson that is shorter than the caudal furcae. The telson margins of *D. rolfei* and *D. testudinea* are apparently unornamented while those of *D. paradoxoides* are setose.

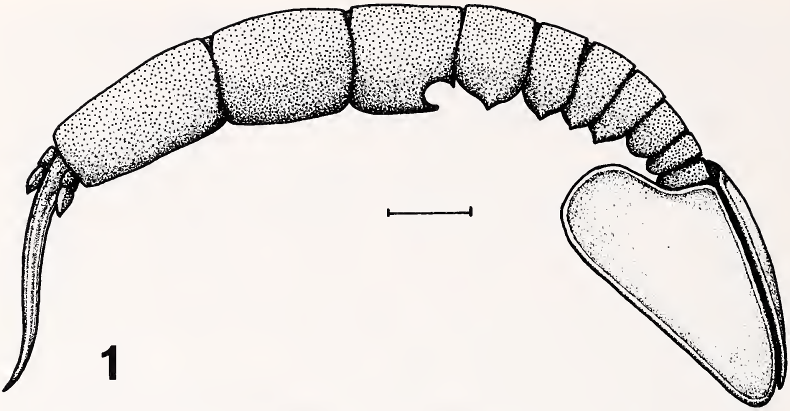
The various specimens assigned to this taxon permit making some suggestions about the morphology of *Dithyrocaris* that are more detailed than those previously made. The typical dorsal view of complete animals, confirms that the axial structures of the carapace did not function as a hinge. Rather, the entire carapace seems to have been a well calcified, rigid structure which, when distorted during burial, tended to yield in areas other than along the axis (Fig. 3.2). Less commonly, the taxon is represented by specimens consisting of lateral views of one carapace valve only (Fig. 3.3). These, we interpret to represent molted fragments of the exoskeleton, perhaps the most durable and, therefore, the most likely molt fragment to be preserved. Finally, a single specimen representing the entire organism is preserved in lateral view with only the right valve of the carapace preserved (Fig. 3.4). This specimen could be interpreted in several different ways. It might represent a normal individual preserved in lateral view or it might represent the entire molted exoskeleton. The flexed position of the abdomen might argue for this interpretation. A third interpretation, however, seems more plausible. This specimen might represent a "softshell" *Dithyrocaris* buried shortly after molting and while the carapace was still flexible enough to articulate somewhat about the axis. This position is reinforced by the observation that, under ultraviolet illumination, various parts of the internal anatomy are visible.

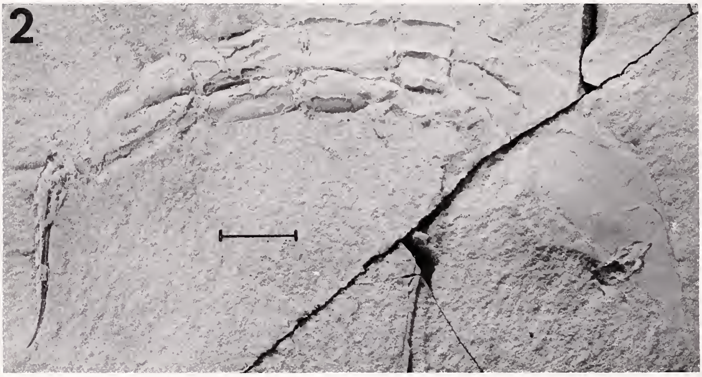
Examination of this latter specimen (UM6225) and another (CM34443) raises some doubt about the number of thoracic and abdominal segments. It would appear that the posterior-most seven segments are each characterized by pleural elements and that only the posterior four are heavily sclerotized. Anteriorad of these seven segments lies a single segment whose tergal outline resembles those of the abdomen but without tergal flaps. This, in turn, is preceded by as many as seven faintly defined segments, decreasing in size regularly toward the anterior. These, clearly, are thoracic segments. The single intervening somite simply cannot clearly be assigned either to the thoracic or the abdominal region, at least until details of the gills or the appendages are discovered. The only tangible evidence, the absence of pleural flaps, suggests placement of the segment in the thoracic region, a position we adopt.

Based on its size, bivalved, dorso-ventrally compressed carapace and ventrally directed sensory and trophic apparatus, *Dithyrocaris rolfei* is interpreted to have been a benthic species (Rolfe, 1969:R309). The absence of terrace lines as found on *D. testudinea* may indicate that while some members of the genus may have been shallowly infaunal in habit (Seilacher, 1973; Schmalfuss, 1978; Briggs and Rolfe, 1984), *D. rolfei* was probably, in large part, epifaunal or, perhaps, plowed through the sediment to the approximate depth of the mesolateral carinae. The absence of appendages and mouthparts in *D. rolfei* makes further trophic interpretation less certain.

Suborder uncertain
Family Sairocarididae Schram, 1973
Genus ***Sairocaris*** Rolfe, 1963
Sairocaris centurion Schram and Horner, 1978
Fig. 4

Diagnosis.—Bivalved phyllocarid. Elongate telson with medial longitudinal carina, longer than pretelson segment, dorsally flexed at pos-





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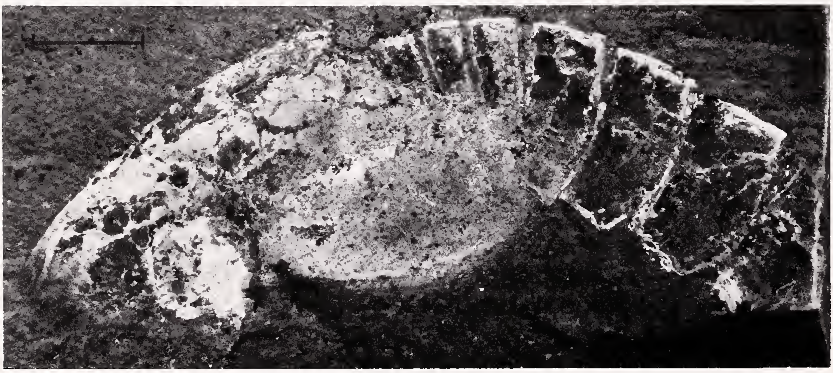

Table 2.—*Representative measurements of* Sairocaris centurion *(in cm).*

Catalog no.	Carapace midline	Abdominal segments							Telson
		a_1	a_2	a_3	a_4	a_5	a_6	a_7	
†UM6179						1.32	1.53	2.15	2.62
†UM6218							.76	1.04	1.37
†UM6289							.59	.88	1.33
†UM6491*	2.40	.52	.58	.67	.85	1.32	1.58	2.08	1.57
†FMNH32088						1.67	1.80	2.57	3.23
†FMNH32089		.36	.40	.47	.54	.87		1.59	2.16
CM34447				.50	.54	1.12	1.30	1.94	2.38
CM34446	3.67	.65	.84	.91					

† From Schram and Horner, 1978.
* Holotype.

terior end. Uropods reduced, blade-like, pretelson segment elongate. Fifth abdominal segment with circular notch in antero-ventral corner of pleuron.

Description.—Bivalved (CM34446, Fig. 4.1, 4.3), carapace strongly alate, thin, smooth, subtriangular in profile, about one-half as long as abdomen. Anterior and ventral margins smoothly convex. Posterior margin strongly sigmoid, concave at mid-dorsum. No rostral or median dorsal plates visible. Entire margin marked by marginal ridge (CM34446).

Three thoracic and seven abdominal segments exposed behind carapace (UM6491). Thoracic segments covered by branchiostegite laterally and ventrally (UM6491, CM34446) when viewed laterally; dorsal surfaces smooth, subequal in length, shorter than first four abdominal segments. Integument of thoracic and abdominal segments finely punctate (UM6491, CM34447, CM34446). Segments increase in length posteriorly; 1 to 4 approximately one-half as long as 5 to 7 and not as tall (UM6491, CM34447). Pleura of first three abdominal segments acuminate along mid-ventral surface. Tergal margins smooth. Pleural margin of fifth segment with prominent notch in antero-ventral corner, notch extends approximately one-third segment length and to height of pleuron on preceding segment. No marginal furrow visible on pleura. Terga as on segment 1 to 3 but longer.

Telson base finely punctate, distinct dorsal flexure distally. Ornamented by longitudinal ridge. Uropods reduced to small ovate appendages visible at base of telson, approximately one-sixth telson length.

No thoracic or abdominal appendages visible. Heavily sclerotized undefinable mass in oral region (UM6491, CM34446). A triangular trace extends postero-ventrally from anterior-most part of carapace approximately one-eighth carapace length.

Materials and measurements.—Measurements, in centimeters, of all *Sairocaris centurion* specimens used in this study are given in Table 2.

Remarks.—*Sairocaris centurion* is easily recognized within the Bear Gulch fauna and appears to be distinguishable from the Scottish Visean

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Fig. 4.—*Sairocaris centurion* Schram and Horner. 4.1, reconstruction showing bivalved nature of the carapace. 4.2, UM6491, holotype. 4.3, CM34446 ultraviolet photographic technique showing the bivalved nature of the carapace. Bars represent 1 cm.

S. elongata on the basis of greater segment heights, much smaller size and more rounded shape of the notch on the fifth pleomere and longer relative telson length and flexure on the latter.

One specimen (CM34446) is of particular interest. Examination of ultraviolet fluorescence photographs of this specimen (Kummel and Raup, 1965) revealed the presence of a bivalved rather than a univalved carapace (Fig. 4.3). This is the only specimen examined from the Bear Gulch that illustrated this feature. *Sairocaris elongata* has not been figured with this feature (Rolfe, 1969; Schram, 1979*a*). That a bivalved carapace has not been observed in previously studied specimens is probably due to the generally poor preservation of this structure and to the orientation of most specimens. Typically, *Sairocaris* is preserved in lateral aspect. Other specimens (especially UM6491) failed to fluoresce. Only CM34446 responded to the ultraviolet wavelengths by fluorescing.

In 1973, Schram erected the Order Hoplostraca (p. 78) to embrace a single family, the Sairocarididae. The basis for distinguishing the order was primarily the absence of a bivalved carapace. He also referred parenthetically to the "distinctive nature of the body tagma" (1973: 78) as being of primary importance in distinguishing the order. The Sairocarididae, in turn, contained two genera—*Sairocaris* and *Kellibrooksia.* This latter genus was described as containing a single species from Mazon Creek (Schram, 1973:80) and was not clearly distinguished from *Sairocaris.* It would appear that the outline of the carapace and relative proportions of the abdominal somites would constitute the primary distinguishing features. Specimens of *Kellibrooksia,* judging from the illustrations by Schram (1973), are not well preserved which renders making distinctions very difficult. Based on our present understanding of *Sairocaris,* and the recognition that it and *Kellibrooksia* are very similar, we would suggest that the Sairocarididae is a distinct family but that the family should properly be assigned to the Archaeostraca. Thus, the Order Hoplostraca becomes void. This conclusion lends some support to Rolfe's suggestion (1969:R328) that *Sairocaris* may be assignable to the Ceratiocarina. The presence of a bivalved carapace would certainly make a stronger argument for this change on purely morphological grounds.

Little is known about the feeding habits of phyllocarids or their habitat requirements. The large abdomen, reduced thorax and apparent absence of pleopods on *Sairocaris centurion* suggest a benthic habit as swimming in phyllocarids is indicated by flattened thoracic and abdominal appendages (Rolfe, 1969). The absence of any appendages means this interpretation is by no means certain. Rolfe's (1969) suggestion that the large mandibles of Paleozoic Archaeostraca were used to chew up large detrital fragments seems to apply to *Sairocaris cen-*

turion. The large sclerotized mass in the oral region of UM6491 and CM34446 probably represents mandibles and would appear to have been capable of handling large pieces of detritus. A similar feature is preserved on a specimen of *Kellibrooksia macrogaster* from the Mazon Creek fauna (Schram, 1973:81, fig. 3).

Subclass Hoplocarida Calman, 1904
Order Palaeostomatopoda Brooks, 1962
Family Perimecturidae Peach, 1908
Genus **Perimecturus** Peach, 1908
Perimecturus rapax Schram and Horner, 1978
Fig. 5

Diagnosis.—Palaeostomatopod with five carinae on posterior surface of carapace and six carinae on abdominal tergites. Terminal spike more than half the length of telson; telson serrate in region of caudal furcae. Uropodal protopod serrate distally; endopod a small spine-like projection; exopod styliform, serrate along distal third of outer margin.

Description.—Carapace dorso-ventrally compressed, approximately as wide as long. Antero-lateral margin evenly convex; mid-dorsal anterior margin concave over rostrum (CM34448, CM34449). Postero-lateral margin slightly convex. Posterior margin sinuous, with mid-dorsal spine (CM34448, CM34450; Fig. 5). Marginal ridge surrounds entire carapace. Rostrum a separate articulated plate, spatulate, axially depressed; one-third the length of the carapace extends beyond carapace margin about one and a half times its width. Posteriorly divergent antennal carinae extend from anterior carapace margin about one-sixth length of the carapace (CM34450). A medial and two lateral pairs of carinae extend anteriorly from the posterior carapace margin about one-third to one-half its length (CM34450, CM34448, CM34449). Medial carina intersects transverse carina that is slightly concave forward at midline becoming more concave laterally, terminates in elements nearly paralleling lateral margins. Anterior-most carapace surface marked by coarse ridges and nodes; entire surface finely punctate (CM34451).

Six abdominal somites, punctate as carapace (CM34451, CM34448, CM34452); subequal in length, slightly wider in mid-abdomen, tapering anteriorly and posteriorly. Pleural margins with marginal ridge continuing to anterior tergal margins; sharp, posteriorly directed postero-lateral spines mark terminations of marginal ridge. Tergal margins straight except near mesolateral carinae with small anterior marginal ridge (CM34451). In plan view, three longitudinal pairs of ridges: one pair straddles the midline; two, closely spaced, parallel the body outline adaxial to pleurae, converging on fifth segment. Node midway between medial and first lateral ridge on segments 1 to 6 (CM34451, CM34448) and on telson (CM34449).

Telson large, marked by marginal ridge (CM34448), a medial and two pairs of convergent lateral ridges, and node near base. Base broadly triangular, axis attenuated into long sharp spine with furcal spine and two or three pairs of subterminal fixed caudal spines (CM34448, CM34451). Styliform uropodal exopods with marginal furrow nearly as long as telson. Outer exopodal margins spined along distal one-third of length. Uropodal bases with prominently spined protopods and endopods (CM34451).

Preserved appendages are short annulate antennules with two visible rami and antennae (CM34450, UM6141 [holotype]). Antennules and antennae subequal in length. Bases with two subequal segments visible (CM34450).

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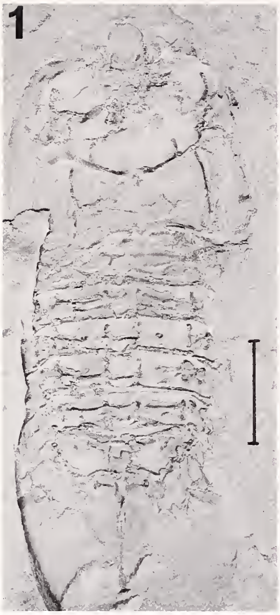

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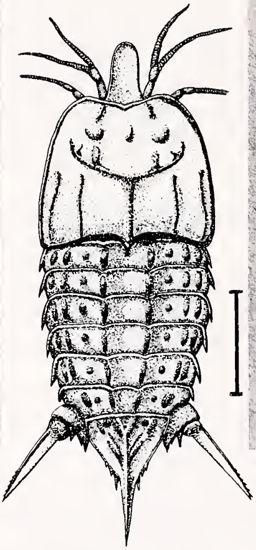

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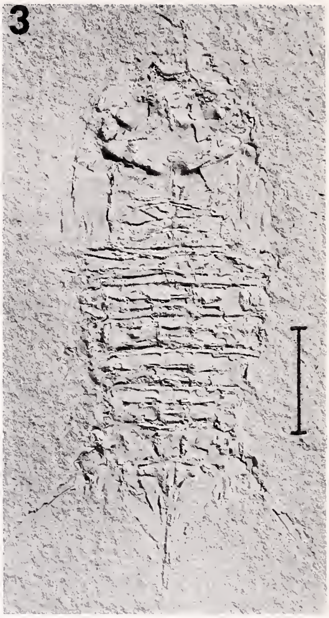

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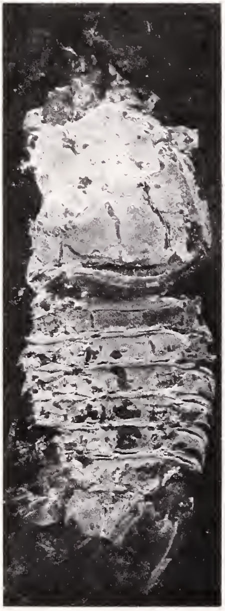

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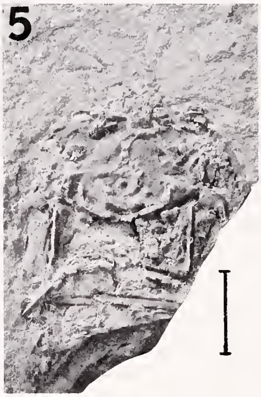

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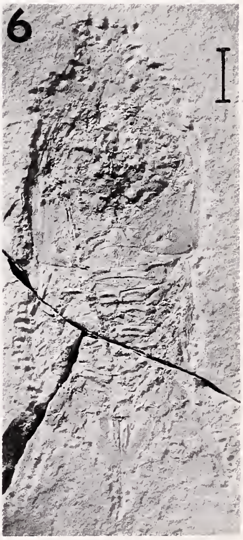

Table 3.—*Representative measurements of* Perimecturus rapax *(in cm).*

Catalog no.	Rostrum	Carapace midline	Total length abdominal segments	Length telson base	Length telson spike	Uropod lateral margin
†UM6141*	.56	2.59	2.83	.99	.80	2.14
†FMNH32090	.37	1.41	1.58	.46		
CM34450		1.85				
CM34451	.48	1.37	1.64	.69	.50	.90
CM34452		2.44	2.79	.82	.67	1.24
CM34448	.53	1.73	2.47	.82		1.08
CM34449	.50	1.86	2.18	.81		1.10

† From Schram and Horner, 1978.
* Holotype.

Materials and measurements.—Measurements, in centimeters, of all *Perimecturus rapax* specimens used in this study are given in Table 3.

Remarks.—The genus *Perimecturus* has only one unquestioned species other than *P. rapax.* Two former members of the genus *P. pattoni* Peach, 1908, and *P. fraiponti* Van Straelen, 1923, have been recognized as tyrannophontids (Schram, 1979*b*). *Perimecturus fraiponti* Van Straelan, 1923, has been reassigned by Schram (1984) to the genus *Tyrannophontes.*

Specimens of *Perimecturus rapax* and *P. parki* from the Scottish Glencartholm Volcanic Beds are preserved most often in dorsal view. This probably reflects the species' strong dorso-ventral compression. At least one specimen from Scotland (Institute of Geological Sciences, Edinburgh (G.S.E.) 5874) is preserved in profile with subchelate thoracopods visible (Schram, 1979*a*). In detail the species seem to differ mainly in the fine points of ornamentation on the carapace, abdomen and especially the tail. The carapace of *P. parki* apparently has no medial carina as found on *P. rapax.* Dorsally, the abdominal ornamentation of *P. rapax* appears to be similar to *Perimecturus parki* (Schram, 1979*a*) with paired carinae straddling the midline and the remaining carinae more lateral in position. The main difference is the pairing of these lateral carinae in *P. rapax* and the presence of a node between the mid-dorsal and lateral carinae (CM34449, Figs. 5.1, 5.2, 5.4).

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Fig. 5.—*Perimecturus rapax* Schram and Horner. 5.1, CM34448. 5.2, dorsal reconstruction. 5.3, CM34451. 5.4, CM34449 ultraviolet photographic technique. 5.5, CM34450. 5.6, UM6141, holotype. Bars represent 1 cm.

The structure of the tail has been recognized as the easiest way to distinguish *Perimecturus rapax* from *P. parki.* The uropods and telson of *Perimecturus parki* are prominently setose. The outer margins of the uropodal exopodite and the posterior telson base margin of this species are smooth, the telson spike is less than one-half the length of the telson base. On *Perimecturus rapax* no setae have been found on the tail apparatus. The distal one-third of the outer margin on the uropodal exopodite is serrate, the telson spike is more than one-half the length of its base and the telson's margin is serrate in the vicinity of the furcae flanking the telson spike.

Perimecturus rapax is interpreted to have been a low level active carnivore in the Bear Gulch area. This conclusion is based on the inferred presence of subchelate thoracopods as found on *P. parki* in Scotland which are indications of rapacious habits (Schram, 1969).

Order Stomatopoda Latreille, 1817
Suborder Archaeostomatopodea Schram, 1969
Family Tyrannophontidae Schram, 1969
Genus ***Tyrannophontes*** Schram, 1969
Tyrannophontes theridion Schram, 1969
Figs. 6–7

1978. *Bairdops beargulchensis* Schram and Horner, p. 398; pl. 1, figs. 3, 5; text-fig. 4.

Diagnosis.—Stomatopod; carapace extends mid-dorsally to about fourth thoracic segment; laterally at least part of sixth thoracic segment exposed. Thorax shows regionalization by size; posterior-most segments, 6–8, taller, longer than anterior segments, only slightly smaller than abdominal segments. Uropodal protopod with two small spikes; exopodite outer margin with articulated spines along distal two-thirds of length; exopodite and endopodite blade-like without diaresis, setose. Telson with terminal spike flanked by spines.

Description.—Carapace thin, smooth, cylindrical, subtriangular in profile, approximately one-half as tall as wide and one-half the length of abdomen. Antero-lateral margin smoothly convex. Posterior margin sigmoid, convex near postero-ventral corner and concave dorsally. Rostrum smooth, sharply pointed, down turned, about one-fourth mid-dorsal length of carapace (CM34454, UM6138). Antennules annulate triramous, base of three segments (CM34455), antennal scale large (UM6022). Margin of carapace with marginal furrow; no other grooves evident. Three thoracic segments exposed laterally posteriad of carapace, two more exposed dorsally (CM34454, UM6138, UM6492). Three posterior-most thoracomeres larger than those anteriorad. Fully exposed somites increase in size posteriorly, smaller than abdominal somites. Pleurae of thoracomeres rounded with marginal rim; terga smooth with marginal furrow, rim (UM6138, CM34454). Four subchelate, subequal thoracopods on anterior thoracic segments. Propodus massive, armed with two rows of unequally sized spines. Row of larger spines more widely spaced than finer row. Dactylus thin, inwardly curved blade, one-half length of propodus, no

Table 4.—*Representative measurements of* Tyrannophontes theridion *(in cm).*

Catalog no.	Carapace midline	Length last 3 thoracomeres	Total abdomen length	Telson	Uropod lateral margin
††FMNH25502	1.19	.83	2.83	1.05	
††FMNH25506			1.76	1.52	.89
††FMNH25507	1.07	.84	2.40		
UM6492	1.71	1.43	4.30	2.20	1.46
*UM6217	2.43		4.98		
UM6138	.78	.62	1.99	.77	
CM34454	.73	.51	1.66	.82	
CM34460	.56	.57	1.63	.74	.60
CM34453	1.17	.89	2.96	1.35	1.05
CM34459	1.22	.94	3.16	1.47	1.19
CM34455	1.20	1.06	3.15	1.58	1.16
CM34461		.75	2.20	1.78	1.12

†† From Mazon Creek fauna.
* Holotype of *Bairdops beargulchensis.*

evidence of spines (CM34456, CM34457, CM34455, CM34458). Carpus, ischiomerus small, subequal in size, basis elongate. Posterior thoracic appendages present but form indistinguishable (UM6492, CM34450).

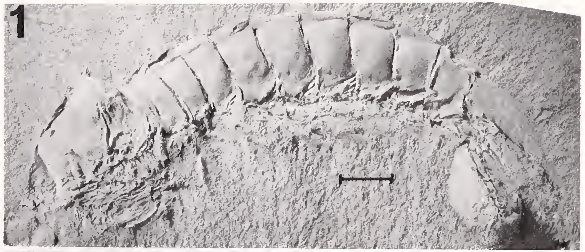
Six subequal abdominal somites, decreasing height posteriorly; pleural lobes subquadrate, corners rounded; posteriorly directed spine on postero-lateral corner of segments 3–5; all with marginal rim and furrow. Terga smooth. Pleopods of segments 1–5 with segmented axis, flattened distally.

Telson broadly ensiform with dorsal carina (UM6492). Telson length about equal to last three abdominal segments, terminal spike flanked by spines. Blade-like uropodal exopodite with articulated spines along distal two-thirds of outer margin (UM6492); marginal furrow present. Endopodite and exopodite blade-like, setose (UM6492, UM6138). Uropodal protopod marked by two spines (CM34454).

Materials.—Specimens of *Tyrannophontes theridion* utilized in this study follow: CM34453–CM34468, UM5174, UM4976, UM6022, UM6138, UM6217 (holotype of *Bairdops beargulchensis*), UM6492, FMNH25502, FMNH25506, FMNH25507.

Measurements.—Measurements, in centimeters, of selected specimens are given in Table 4.

Remarks.—*Tyrannophontes theridion* was named by Schram in 1969. The species was represented by well-preserved material in concretions and was part of the Essex fauna of Mazon Creek. The species was envisioned to belong to a primitive suborder of stomatopods, the Archaeostomatopodea, exhibiting regionalization of the thorax, and a tail apparatus with unisegmental protopods, blade-like exopods and endopods, and a triangular telson (Schram, 1969:260). A recent re-examination of the original material used to describe the species led to the conclusion that the propodus on the subchelae was more massive than originally described, and that the uropodal exopods and endopods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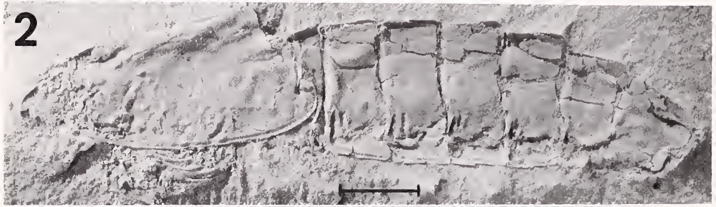
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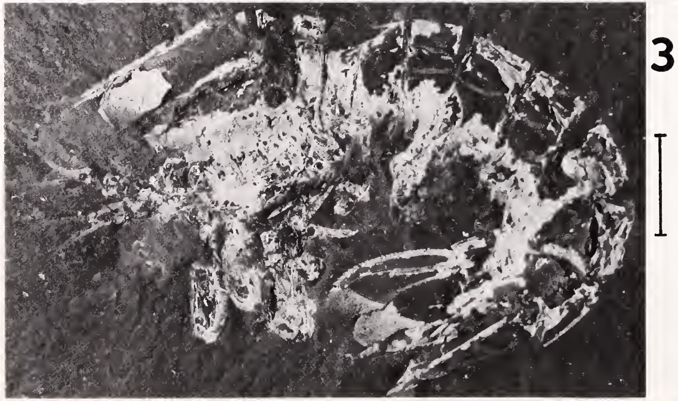
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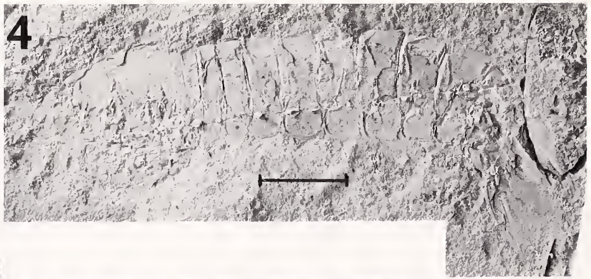
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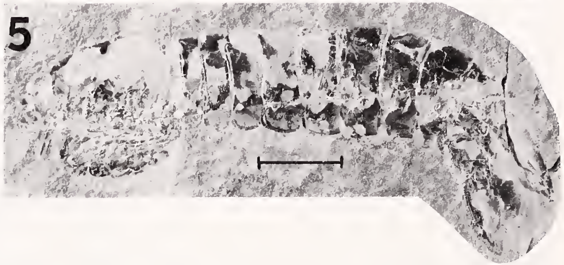
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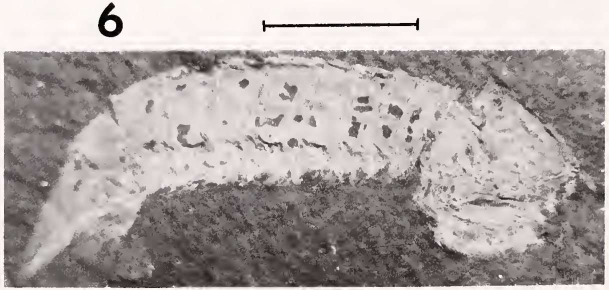
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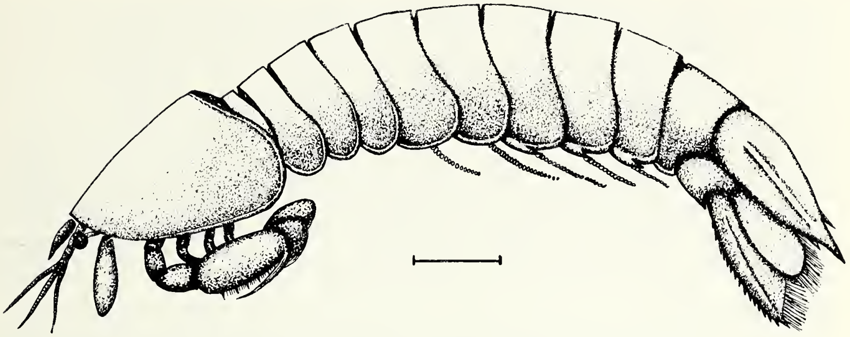

Fig. 7.—Lateral reconstruction of *Tyrannophontes theridion* Schram. Bar represents 1 cm.

were less narrow (Schram, 1984:202). These revisions are supported by observations made on the Bear Gulch specimens of *Tyrannophontes theridion.* Bear Gulch specimens show more morphological detail than those from Mazon Creek for preservational reasons. Most Bear Gulch specimens are preserved in micrite with mineralized exoskeletal material still present. Mazon Creek specimens are preserved as impressions in more coarsely grained ironstone nodules. Morphologically, specimens of *T. theridion* from the Bear Gulch differ little from the revised concept (Schram, 1984) of the Mazon Creek material except for size (Figs. 6 and 7). Bear Gulch specimens may reach a larger size than any reported from Mazon Creek.

Bairdops beargulchensis Schram and Horner, 1978, was erected as a taxon based on fragmentary material from the Bear Gulch. This taxon was envisioned to represent a medium to large palaeostomatopod with a massive propodus, broadly blade-like uropodal exopods and endopods, and a triangular telson with a terminal spike flanked by furcal lobes. Newer, more complete specimens (CM34462, CM34453 (Figs. 6.4, 6.5), CM34459, and CM34455 (Fig. 6.3)), indicate that these features are found on specimens exhibiting undoubted *T. theridion* characters. These specimens exhibit a distinctly regionalized thorax with three fully exposed thoracic segments posterior to the carapace, a broad propodus armed with a double row of spines opposed by a thin, smooth

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Fig. 6.—*Tyrannophontes theridion* Schram. 6.1, cast of UM6492. 6.2, cast of UM6217. 6.3, CM34455 ultraviolet photographic technique showing details of antennae, thoracopods and tail ornamentation. 6.4, CM34453 whitened. 6.5, CM34453 unwhitened. 6.6, CM34454 ultraviolet photographic technique. Bars represent 1 cm.

dactylus, and a tail apparatus with broad blade-like uropodal elements and a triangular telson terminating in a spike and flanked by caudal spines. They differ from published descriptions of *T. theridion* in that the outer margins of the uropodal exopodite are armed with articulated spines, the posterior uropodal and telson margins are sometimes setose, and the terminal spike of the telson is flanked by furcal lobes. Some or all of the characters may or may not occur on any one specimen. The conclusion, based on observations of these specimens, is that *Bairdops beargulchensis* is a junior synonym of *Tyrannophontes theridion.* Differences from specimen to specimen are attributed to the vagaries of preservation.

The revised description of *Tyrannophontes theridion* is of particular interest when comparing *T. theridion* to the newly described *Gorgonophontes peleron* Schram, 1984. Schram (1984) pointed out that some anatomical details necessary for morphological comparisons of *T. theridion* to *Gorgonophontes peleron* Schram, 1984, are not available in the Mazon Creek material. Comparisons of Bear Gulch *T. theridion* material to *Gorgonophontes peleron* suggests similarity of the species. Some Bear Gulch specimens, especially CM34455 (Fig. 6.3), demonstrate that the propodus of *T. theridion* had two rows of spines, one with closely spaced, fine spines, one with more widely spaced and larger spines. This feature is similar to *G. peleron* Schram, 1984. The tails of specimens of *T. theridion* from Bear Gulch differ from those of *G. peleron* in the details of their ornamentation and absence of a diaresis. They are otherwise similar. The presence of a terminal spike on the tail of *T. theridion* at Bear Gulch is significant because this is one of the diagnostic features for the genus *Gorgonophontes* as described by Schram (1984). The main morphological features remaining which separate *Tyrannophontes theridion* from *Gorgonophontes peleron* are the size of the postero-lateral carapace wings, the shape of the abdominal pleurae, presence or absence of a diaresis on the uropodal exopod, and the relative lengths of the propodus and dactylus of the thoracopods.

It should be noted here that many of the details of *Tyrannophontes theridion* morphology were made more clear by ultraviolet radiation fluorescence photography of the specimens. Many *T. theridion* specimens were particularly responsive to this technique but CM34454 and CM34455 (Figs. 6.3 and 6.6) were especially useful for study of thoracic segment regionalization, propodus shape and armament, pleural margins, and details of tail morphology.

The presence of armed thoracopods suggest a benthic, predaceous habit similar to that of modern stomatopods for these organisms (Schram, 1969, 1979*b*).

Order Aeschronectida Schram, 1969
Family Aenigmacarididae Schram and Horner, 1978
Genus ***Aenigmacaris*** Schram and Horner, 1978
Aenigmacaris cornigerum Schram and Horner, 1978
Figs. 8–9

Diagnosis.—Malacostracan with thinly sclerotized carapace; prominent anteriorly directed mid-dorsal spine; antero-dorsal and antero-ventral spines present. Ventral margins of abdominal pleura triangular, smooth. Third abdominal segment with strong dorsal flexure.

Description.—Carapace thin, smooth, subquadrate in lateral view, about twice as long as high. Anterior with prominent anteriorly directed mid-dorsal spine arising anterior to midlength, extends to anterior carapace margin (CM34465, CM34466, UM6191, UM6146). Antero-dorsal and antero-ventral spines define limits of anterior carapace margin. Ventral margin slightly convex, greatest curvature posterior to midlength. Posterior margin sigmoid, concave at mid-dorsum. Endophragmal skeleton often visible, with 8 subequal segments apparent, no pleurobranchial openings visible (CM34465, CM34466, UM6191, UM6146).

Thinly sclerotized abdomen approximately twice length of carapace. Six segments present; segments 1 to 3 and 4 to 6 increase in length posteriorly. Third and sixth tergites longer than remaining four; overall decrease in height posteriorly. Pleurae ventrally pointed, triangular in outline; margins smooth. Terga of third segment strongly flexed ventrally. Telson poorly preserved, apparently elongate with mid-dorsal carina, shape of margins unknown (CM34467; Fig. 8.1). One specimen (CM34467) with uropods about one and a half times longer than telson with smooth outer margins, no other details visible.

Mandible heavily sclerotized (CM34465, CM34466, CM34467, UM6146). Thoracopods similar, long, with strong proximal elements. Ischium and merus marked by rows of setal (?) pits along outer margin. Distal elements more slender; no apparent developments of chelae. Pleopods present but poorly preserved (CM34467, UM6191), stenopodal, five segments, most proximal segment short, next two segments longer, two distal segments very short.

Intestine straight, dorsally positioned, anus immediately anterior to base of telson (UM6191).

Materials and measurements.—Measurements, in centimeters, of all specimens of *Aenigmacaris cornigerum* used in this study are given in Table 5.

Remarks.—Specimens are preserved as thin, mineralized material in profile on bedding planes with only a small amount of relief. Preservation of the main body and proximal portions of the thoracopods is often very good, but other appendages and the tail are generally not well preserved. Those specimens studied which exhibited pleopods had only the appendage bases visible on all five abdominal segments (CM34467) or complete appendages on only one segment (UM6191). The slender, elongate, well-sclerotized, and jointed legs imply a benthic habit (Manton, 1977).

In the specimens preserved with the intestine visible (UM6112 and UM6191), no coarse fragments of material are visible. The gut material

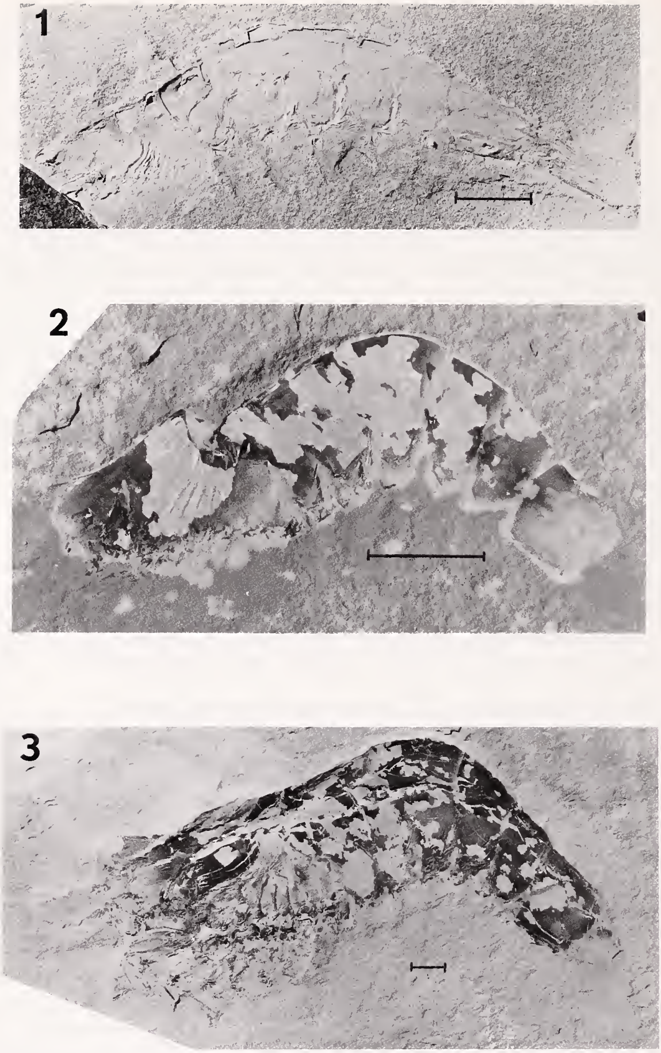

Fig. 8.—*Aenigmacaris cornigerum* Schram and Horner. 8.1, CM34467. 8.2, UM6146, holotype, counterpart to Schram and Horner, 1978, pl. 2, fig. 1. 8.3, CM34465. Bars represent 1 cm.

appears to be identical to the matrix in which the specimens were preserved suggesting a detrital feeding habit. This interpretation is supported further by the absence of chelae on any of the thoracopods. These animals had no limbs adapted to grasping or tearing apart prey.

Table 5.—*Measurements for* Aenigmacaris cornigerum *(in cm).*

Catalog no.	Carapace length	Carapace height	Carapace horn length	Abdominal segment lengths					
				a_1	a_2	a_3	a_4	a_5	a_6
UM5889	2.18	1.95	1.02	.54	.57	.60	.47	.30	.50
UM6112				.69	.96	.87	.94		
*UM6146	1.80	.60	.26	.44	.72	.89	.66	.59	.82
UM6191	3.69	1.75	.75	.75	.97	1.25	1.03	1.04	1.42
CM34468		2.24		.84	.94	1.72	1.17	1.21	1.60
CM34465	4.25	2.53	.79	.69	1.00	1.63	1.27	.88	1.58
CM34466	3.29	1.70	.57	.45	.88	1.46	.80	.92	1.39
CM34467		1.26	.38	.64	1.07	.95	.87	.65	1.22

* Holotype.

The thin nature of the carapace reflected by the visibility of the endophragmal skeleton in specimens is typical of the genus (see Schram and Schram, 1979). While larger than *Aenigmacaris minima* Schram and Schram, 1979, the characteristics of preservation and morphology indicate that *Aenigmacaris* was a wide ranging genus in Carboniferous rocks of the western United States.

Order Aeschronectida Schram, 1969
Family Aratidecthidae Schram, 1978
Genus *Crangopsis*
Crangopsis eskdalensis (Peach, 1882)
Figs. 10–11

1882. *Palaeocrangon eskdalensis* Peach
1903. *Palaeocrangon eskdalensis* Peach and Horne
1908. *Crangopsis eskdalensis* (Peach). Peach
1911. *Crangopsis eskdalensis* (Peach). Woodward
1969. *Crangopsis eskdalensis* (Peach). Brooks
1969. *Crangopsis eskdalensis* (Peach). Schram

Diagnosis.—Hoplocarid, no rostrum, subtrapezohedral carapace; antennules well developed, prominent antennal scale; pleuron of first abdominal segment covered by posterior extension of carapace and inflated pleuron of second abdominal segment.

Description.—Small, carapace subtrapezohedral in outline, thin, approximately one-half length of abdomen. Posterior margin sigmoid; convex postero-ventral margin, concave dorsally. No rostrum, spines, carina or grooves other than faint marginal ridge on postero-ventral margins (CM34469-A, CM34469-B, Figs. 10.2 and 10.3).

Six abdominal segments present. Pleuron of first segment hidden by branchiostegal flap of carapace and anterior portion of broadly rounded pleuron of second abdominal somite (CM34469-C). Pleuron of third segment smaller than second segment; rounded

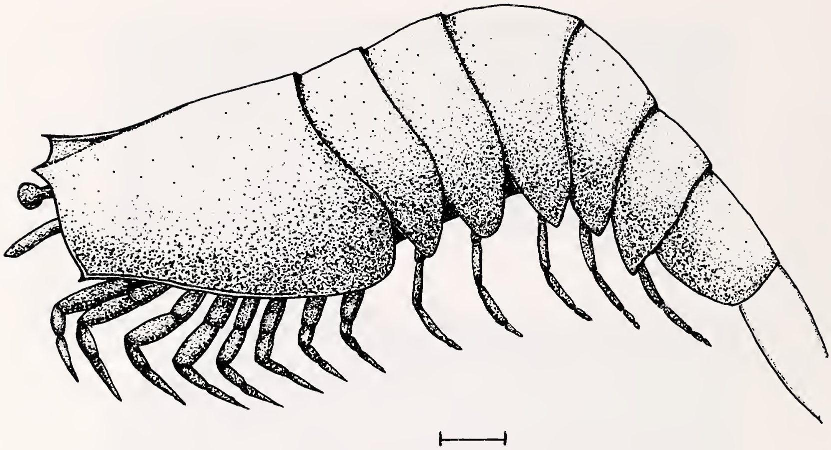

Fig. 9.—Lateral reconstruction of *Aenigmacaris cornigerum* Schram and Horner. Bar represents 1 cm.

and attenuated posteriorly. Pleura of fourth and fifth segments forms a notch along posterior margin of segment (CM34469-B). Small marginal ridge borders the four pleura; terga and pleura otherwise smooth (CM34469-B). Terga of first four segments subequal in length, fifth and sixth increase in length. Telson apparently spike-like, uropods with two subparallel carinae (CM34469-A).

Peduncle of antennule with three segments; each narrowing terminally (CM34469-A). Antennules appear to be short, biramous. Blade-like antennal scale, longer than antennule base (CM34469-A). No other appendages preserved.

Materials and measurements.—Measurements in centimeters of all *Crangopsis eskdalensis* used in this study are given in Table 6.

Remarks.—The specimens found in the Bear Gulch which have been studied and assigned to this species are from a group of shrimp preserved on a single, broken-up slab of rock (CM34469). Preservation of most of the individuals is poor but three of the best specimens were utilized to produce the reconstruction (Fig. 11) shown.

The Bear Gulch specimens of *Crangopsis eskdalensis* differ from published descriptions of other species in similar, aeschronectid genera in a variety of readily distinguishable ways. *Kallidecthes* species were larger animals than the *C. eskdalensis* specimens studied. They had longer antennules and antennae than *Crangopsis eskdalensis,* a short rostrum and the pleuron of the first abdominal segment was not covered by the carapace and pleuron of the second abdominal segment (Schram, 1979*a*:237). *Aratidecthes* species were moderate sized organisms like *Kallidecthes.* They possessed enlarged antennules, had no rostrum and only a slightly enlarged pleuron on the second abdominal segment (Schram, 1969:253). *Crangopsis socialis,* like species of *Kallidecthes*

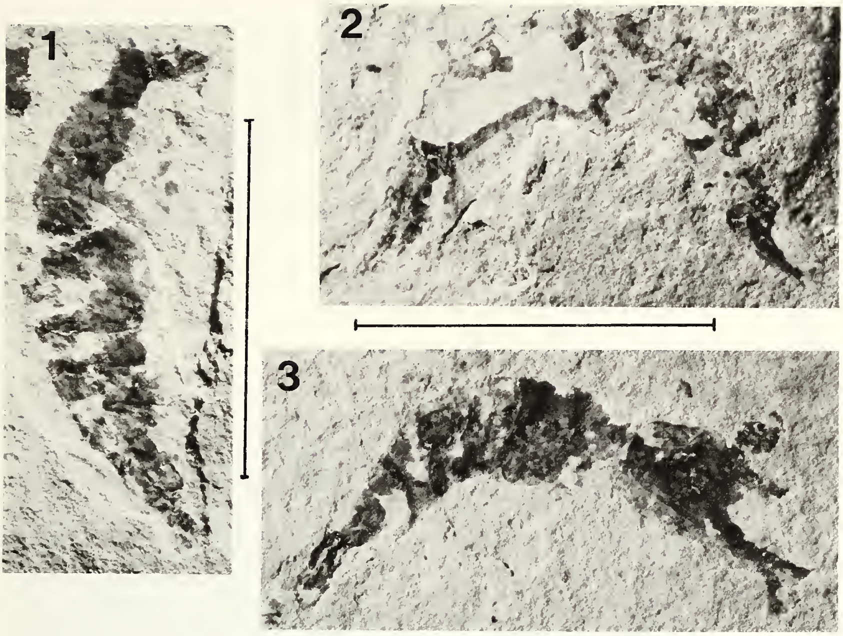

Fig. 10.—*Crangopsis eskdalensis* (Peach). 10.1, CM34469-C. 10.2, CM34469-A. 10.3, CM34469-B. Bars represent 1 cm.

and *Aratidecthes,* was larger than *C. eskdalensis.* It is distinguishable from *C. eskdalensis* on the basis of possession of reptantian-like thoracopods, more alate carapace, a relatively longer length of its first abdominal segment, and the attenuated nature of the postero-ventral corners of the abdominal pleura on segments 3 to 5 in *C. socialis* (Schram, 1979*a*). *Kallidecthes* and *Aratidecthes* species and *C. socialis* appear to have led solitary lives whereas the *Crangopsis eskdalensis*

Table 6.—*Representative measurements of* Crangopsis eskdalensis *(in cm).*

Catalog no.	Carapace	Total abdomen	Abdominal somites					
			a_1	a_2	a_3	a_4	a_5	a_6
†GSE5007	.80	1.98	.14	.42	.23	.23	.25	.70
CM34469-A	.45	.75	.07	.22	.15	.20	.14	.17
CM34469-B	.73	1.06	.12	.25	.12	.18	.14	.25
CM34469-C		1.08	.13	.25	.11	.13	.14	.32

† Schram, 1979*a*. Lectotype *Crangopsis eskdalensis* from Glencartholm fauna.

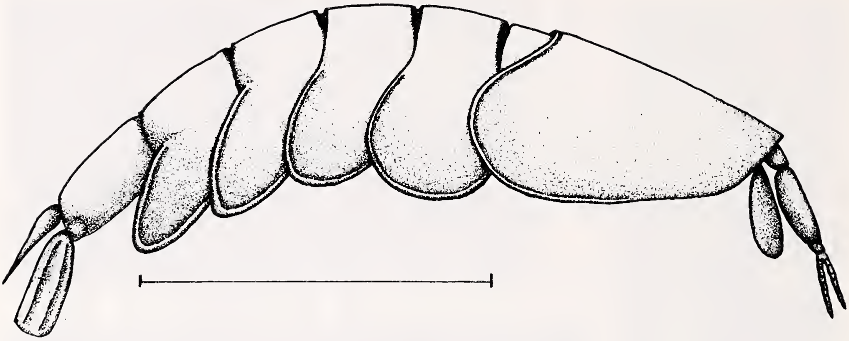

Fig. 11.—Lateral reconstruction of *Crangopsis eskdalensis* (Peach). Bar represents 1 cm.

specimens from the Bear Gulch and the Glencartholm Volcanic Beds in Scotland are found in "schools" (Schram, 1969, 1979*a*:39). It is interesting to note that all the larger aeschronectid genera and *Crangopsis socialis* show signs of solitary benthic adaptations, especially in thoracopod structure, while *C. eskdalensis* was smaller, gregarious, and perhaps nektonic in habit. *Crangopsis eskdalensis* may, indeed, represent adult forms but it seems only prudent to recognize that they may be natant forms as is suggested by Schram and Horner (1978).

Subclass Eumalacostraca Grobben, 1892
Superorder Eocarida Brooks, 1962
Order Eocaridacea Brooks, 1962
Family Belotelsonidae Schram, 1974
Genus **Belotelson** Packard, 1886
Belotelson magister (Packard, 1886)
Fig. 12

Diagnosis.—Eumalacostracan, shrimp-like in overall appearance, with large, smooth carapace; rostrum long; 8 pairs of long, subequal, achelate thoracopods.

Description.—Carapace thin, smooth, subquadrate approximately twice as long as high. Anterior margin with deep, well-defined optic notch (UM6495, CM34470, Fig. 12); ventral margin slightly convex. Posterior margin nearly straight mid-dorsally and strongly convex near postero-ventral corner, projected over pleural lobe of first abdominal segment. Rostrum ensiform with marginal fold and mid-dorsal ridge; approximately one-half length of carapace. Carapace with narrow marginal ridge and furrow on posterior and ventral margin. Endophragmal skeleton visible (UM6495) as postero-dorsally inclined ridges and grooves on carapace.

Abdomen about as long as cephalothorax; five segments decreasing in length posteriorly; sixth elongate. Pleura of first five segments well developed, reniform anteriorly, becoming orbiculate posteriorly, nearly one-half height of the segment; inclined postero-

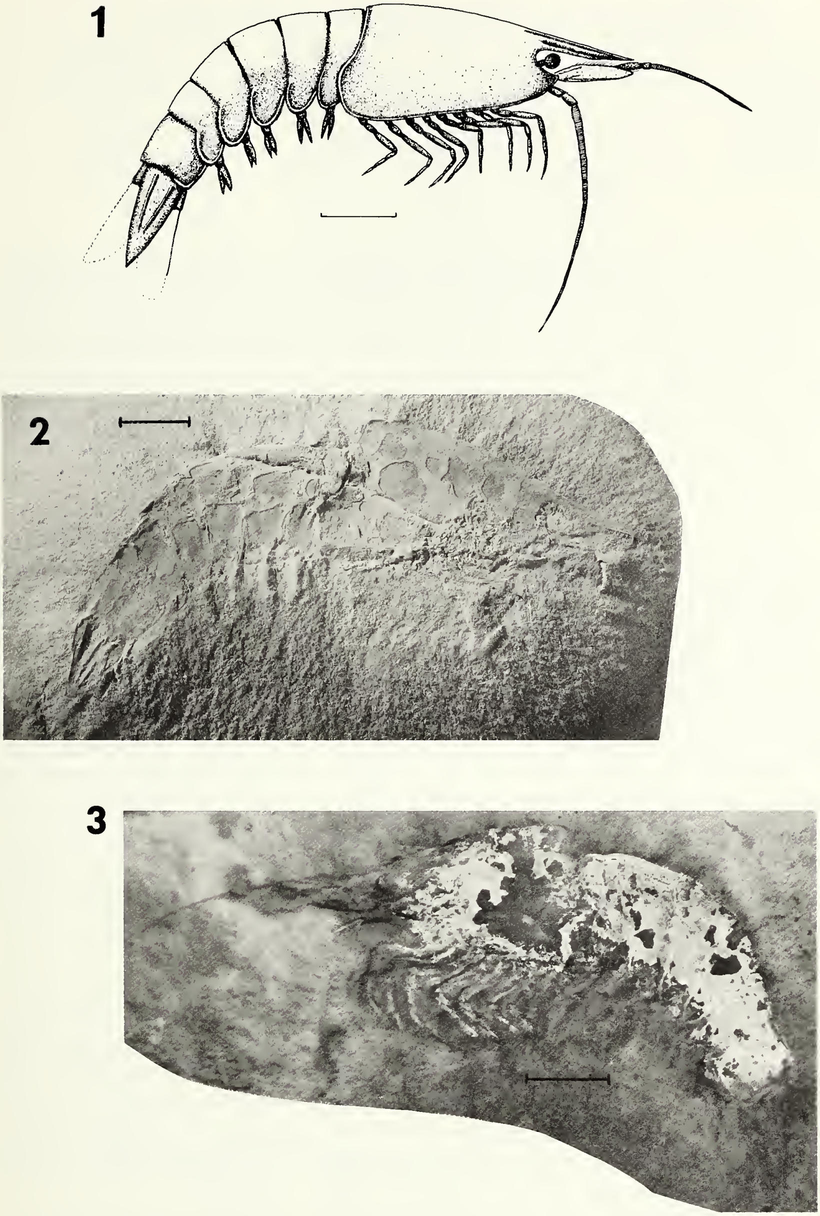

Fig. 12.—*Belotelson magister* (Packard). 12.1, lateral reconstruction. 12.2, UM6495. 12.3, CM34470 ultraviolet photographic technique. Bars represent 1 cm.

Table 7.—*Representative measurements of* Belotelson magister *(in cm).*

Catalog no.	Carapace length	Rostrum length	Body length (optic notch to telson base)
UM5889	2.90	1.05	4.27
UM6495	4.06	1.50	6.24
CM34470	3.57	1.41	6.47

ventrally. Sixth pleuron subquadrate with rounded corners. Distinct marginal ridge and furrow on pleura, otherwise smooth. Terga smooth. Telson longer than sixth segment (UM6495), triangular outline marked by a medial ridge and two lateral grooves. Uropodal exopod lateral margins smooth, apparently tapering posteriorly; no other features visible.

Appendages poorly preserved. Antennule biramous, base with at least two segments, distal element small. Antenna long, single annulate flagellum; at least two segments in base, distal element shorter. Large blade-like antennal scale setose on inner margin (CM34470). Eye apparently stalked, round. Eight pairs of long, similar, achelate thoracopods. Pleopods poorly preserved with large base, blade-like exopod and endopod.

Materials and measurements.—Measurement, in centimeters, of all *Belotelson magister* specimens used in this study are given in Table 7.

Remarks.—Specimens of *Belotelson magister* found in the Bear Gulch Limestone are generally preserved as mineralized impressions and/or casts lying on their sides. This consistent feature of their preservation is unfortunate because no specimens reveal the structure of the animal's ventral surface. Specimens available from Illinois (Schram, 1974) reveal the structure of the mouthparts, development of a branchiostegal chamber, and specialization of the thoracic sternites in a fashion parallel to that of modern reptantian decapods. Despite the prominent nature of the thoracopods the exact structure of their bases is obscured in all the specimens from Illinois and Montana and remains undescribed. *Belotelson traquairi* (Peach) Schram, 1969, from the Glencartholm fauna of Scotland is also imperfectly preserved in this region (Schram, 1979*a*). Another feature not preserved because of the preservational orientation in the Bear Gulch specimens is the distinctive mid-dorsal pore found in both *B. magister* and *B. traquairi.*

None of the specimens studied exhibited details of the pleopods. Specimens CM34470 and UM6495 suggest by the fracture pattern of the rock the presence of short, paired appendages on abdominal segments 1 to 5 but no details of the structures are visible (Fig. 12). Similarly, the exopods and endopods of the tail are simply not preserved. These features may have been too delicate to preserve, but it is the preservation of just such fine features for which the Bear Gulch Limestone is notable.

The anatomical similarity of *Belotelson* to modern crayfish and lobsters suggests the groups occupied similar habitats as bottom dwelling scavengers (Schram, 1974). Absence of chelipeds, however, would

Table 8.—*Near-shore marine crustacean assemblages of the Carboniferous. Analogous taxa are on the same line, with lack of corresponding taxon indicated by a dash.*

Trophic level	Dinantian Glencartholm	Mississippian Bear Gulch	Pennsylvanian Essex fauna Mazon Creek
Rapacious carnivores	*Perimecturus parki*	*Perimecturus rapax*	—
	Bairdops elegans	—	—
	—	*Tyrannophontes theridion*	*Tyrannophontes theridion*
Scavenger low-level carnivores	*Belotelson traquairi*	*Belotelson magister*	*Belotelson magister*
	Pseudogalathea macconochiei	—	—
	Pseudotealliocaris etheridgei	—	*Mamayocaris jaskoskii*
Filter feeders	*Crangopsis eskdalensis*	*Crangopsis eskdalensis*	*Kallidecthes richardsoni*
	Anthracophausia dunsiana	—	*Anthracophausia ingelsorum*
	—	—	*Peachocaris strongi*
	—	—	*Essoidea epiceron*
	Sairocaris elongata	*Sairocaris centurion*	*Kellibrooksia macrogaster*
	—	—	*Ceratiocaris* sp.
	Anthracocaris scotica	*Dithyrocaris rolfei*	*Dithyrocaris* sp.
	—	—	*Cryptocaris hootchi*
	—	—	*Hesslerella shermani*
	Joanellia elegans	*Aenigmacaris cornigerum*	—

Modified from Schram, 1981.

probably rule out low-level predation. The prominent reptantian-like thoracopods and well-developed antennae are especially suggestive of this interpretation. The occurrence of such an organism in anaerobic sediments deposited in a water column believed to be generally hypersaline at the base (Williams, 1981) suggests that *B. magister* lived in localized patches of suitable habitat within this sedimentary environment or that individuals were transported in from surrounding areas.

DISCUSSION

The Bear Gulch malacostracan fauna is of interest because of the quality of its preservation and its diversity. The excellent preservational quality of chitinous and phosphatic residues in fossils of this unit is attributed to the rapid accumulation of very fine-grained carbonate sediments in an area of restricted circulation where the level of available oxygen in the pore spaces of the sediments was extremely low. Preservation of malacostracan material is good enough to allow some internal organs, for example the intestine of *Aenigmacaris cornigerum,* to be seen. However, fine details of anatomy are often lacking in otherwise good specimens. Appendages, for instance, while often present, are difficult to see clearly upon close inspection. Ventral surfaces are almost never visible because almost all specimens are preserved either in profile or with the dorsal surface exposed and hiding the ventral. Some of these shortcomings were reduced by maximizing the detail that is preserved by the use of ultraviolet photographic techniques (see "Remarks" in species descriptions of *Sairocaris centurion* and *Tyrannophontes theridion*). In contrast to chitinous and phosphatic material, calcareous fossils were preserved only as casts and molds. Calcareous skeletons were apparently preferentially dissolved by pore waters (Williams, 1981).

Diversity in this malacostracan assemblage is high enough to embrace the four basic feeding types found in Paleozoic Crustacea; rapacious carnivores, scavengers, filter feeders, and algal-detrital feeders (Schram, 1981). Species assignments to the different feeding types are based on analysis of the functional morphology of appendages and by analogy with modern forms. These interpretations are summarized in Table 8.

The abundance of specimens and the diversity of the Bear Gulch fauna and flora allow some analysis of the trophic structure of the area in which these organisms lived. Malacostracans represent an intermediate trophic level in the food web of this area. Algal and bacterial mats and plankton represented the primary producers for this system. These organisms, along with sponges, provided cover and/or attachment sites for invertebrates and vertebrates. There is little or no evidence to suggest the presence of frame builders such as corals and bryozoans. The presence, in the water column of filter feeding shrimp, such as *Crangopsis eskdalensis,* suggests that plankton were present, despite their absence in the fossil record (Table 8). *Sairocaris centurion, Dithyrocaris rolfei,* and *Aenigmacaris cornigerum* were detrital and perhaps algal consumers living at the sediment-water interface. None possessed the stout appendages necessary for scavenging or predation. *Belotelson magister* was apparently a scavenging species. *Perimecturus rapax* and *Tyrannophontes theridion* were higher level consumers as evidenced by their specialized grasping thoracic appendages. The malacostracans, in turn, were fed upon by fish. An entire 50 mm long *Tyrannophontes theridion* was found in a 150 mm coelecanth, *Caridosuctor populum.* Whole shrimp have been found in three species of sharks (Lund, personal communication). Shrimp parts are often found in fish coprolites throughout the study area.

The diversity, taxonomic composition, habitat, and stratigraphic position of the Bear Gulch malacostracan fauna are of particular interest because of their relationship to other Carboniferous malacostracan assemblages in other parts of the world. The malacostracan faunas from the Glencartholm Volcanic Beds (Visean) in Scotland and the Mazon Creek (Westphalian) in Illinois are from sites of unusually good preservation. When compared to the Bear Gulch fauna (Table 8) striking similarities in diversity, taxonomic composition, habitat, and trophic position are apparent. This phenomenon of assemblages of related species occupying similar trophic positions and habitats over wide geographic areas and relatively long geologic time (70–80 million years) has been discussed by Olsen (1966). He applied the term chronofauna to assemblages exhibiting relatively little change in their ecological relationships or taxonomic composition over time. Schram and Horner (1978) made reference to the persistence of the near-shore marine malacostracan assemblage represented by the Bear Gulch, Glencartholm, and Mazon Creek Essex faunas. Schram (1981) gave a good summary of the relationships found within these three faunas and how their structure changed over time and space (Table 8). In general, species within a genus or a related genus are found living in similar habitats but are separated geographically and stratigraphically. For instance, at Bear Gulch *Perimecturus rapax* is found, not *Perimecturus elegans* of the Glencartholm fauna, and the Bear Gulch's *Sairocaris centurion* has a functional counterpart in a related genus, *Kellibrooksia macrogaster,* at Mazon Creek. At a higher taxonomic level, the more progressive stomatopods replaced their trophic equivalents, the rapacious palaeostomatopods, in the Westphalian Mazon Creek assemblage after appearing and coexisting with the palaeostomatopods at Bear Gulch. The true nature and sequence of species changes from fauna to fauna and over time in North America and western Europe must remain obscure due to the lack of time equivalent diverse fossil assemblages to which these faunas can be compared. The rarity of the special conditions necessary to produce high quality preservation of large numbers of individuals may preclude many new faunal comparisons.

In addition to strictly biological interpretations about the study area during the time of deposition, Bear Gulch fossils combined with sedimentological and stratigraphic information have much to contribute to our understanding of the physical conditions under which the sediments of the Bear Gulch Limestone Beds were deposited. Paleogeographic studies of Montana and Wyoming indicate that the Williston Basin and the eastern portion of the Big Snowy Trough were filling progressively westward with near-shore and off-shore sediments while the Bear Gulch Limestone Beds were being deposited. To the south, the Southern Montana Arch was rising, shedding clastic materials northward into the Big Snowy Trough (Sando et al., 1975; Maughan, 1984). Black shale and limestone were deposited along the axis of the shrinking trough (Sando et al., 1975; Williams, 1981; Maughan, 1984).

The region was tropical during the Late Mississippian and Early Pennsylvanian (Scotese et al., 1979). The deposition of sediments composed of algal- and bacterial-generated micritic muds (Williams, 1981) is typical of tropical conditions as are the clays found in the Bear Gulch Member (Schopf, 1980:196). The rapid deposition of the Bear Gulch Limestone Beds, demonstrated by abundant dewatering faults, numerous and diverse well-preserved fossils, and the short period during which deposition occurred (Williams, 1981), lend further evidence to the high biological productivity rate associated with tropical habitats.

Water depth in the area of Bear Gulch Limestone deposition was generally shallow. Certainly the mats of cyanobacteria and noncalcareous algae found preserved in the sediments lived within the photic zone. A distinct decrease in total organic carbon from marginal to basinal areas of deposition was documented by Williams (1981, table 1). She also considered the exposed sections of the limestones of the Bear Gulch Member to be complete. This shallowing upwards sequence represents about 35–40 m in the main portion of the section exposed at Potter's Creek Dome, with much thinner outcrops, 2 m or less, to the south, east, and west. If the section is complete, then conditions do appear to have been shallow, even in the deepest part of the basin, at the time of deposition.

Wave and current energy levels responsible for deposition of Bear Gulch Limestone sediments are interpreted to have been very low because of the very fine ripple marks in the micritic sediments (Williams, 1981) and the small size of carbonate and clastic sediments in the rocks. Rippling of thin laminations composed of skeletal grains and micrite throughout otherwise massive beds implies a variable, but still low, level of current activity. The presence of occasional platy shales and silts between massive limestones (Williams, 1981) may denote the potential for higher currents dominating the basin at times, or the incursion of the clastic source which eventually engulfed the area with a deltaic sequence.

The pattern of water circulation within the area where the Bear Gulch Limestone Beds were deposited is not easy to deduce. Schopf (1980: 98–112) discussed the possible patterns for flow of waters in a basin. The absence of any circulation would lead to a stagnant, anaerobic water column. The rich nektonic and benthic fossil assemblage of the Bear Gulch Limestone Beds rules out that possibility. The two remaining possible patterns are termed estuarine and Mediterranean. Estuarine flow is characterized by basins in which the rate of inflow of water is much greater than the rate of evaporation in the basin. Mediterranean type basins experience a greater rate of evaporation than inflow of water. Mediterranean basins tend to have a water column with elevated salinities at the base, high pO_2, and low nutrient levels. Sediments in these basins tend to be high in $CaCO_3$ and low in organic carbon (Schopf, 1980). The basin in which the Bear Gulch Limestone Beds were deposited seems to have exhibited a restricted Mediterranean type circulation pattern. The interpreted geographical site of deposition of the Bear Gulch would lie near the southern limit of the predictable low precipitation and high evaporation region characterizing the Mediterranean climate (Scotese et al., 1979). Total organic carbon of the $CaCO_3$ rich sediments is generally low, from 0.5 to 1.5% (Williams, 1981). The input of clastics into the area, and probably of freshwater to compensate for evaporation, was low as evidenced by 5 to 8% quartz silt content (Williams, 1981) in the Bear Gulch Beds. The general absence of benthic organisms with strict open marine requirements, that is, corals, bryozoans, and most echinoderms, coupled with the abundance of somewhat more salinity tolerant near-shore marine benthos, the crustaceans, cephalopods, and sponges, suggests that bottom conditions in the main basin were not normal marine in nature but somewhat hypersaline. Brackish and freshwater forms are found only in southern, marginal facies of the unit's outcrop pattern (Lund and Horner, 1979; Williams, 1981).

Water temperature in the basin was almost certainly warm as indicated by the tropical position and shallow depth of the basin. Temperature apparently did not rise so high as to deplete oxygen levels to intolerably low levels because an abundant open marine fauna existed within the basin.

The oxygen level of the water column within the basin, though not intolerable, may have been low and even lower yet in the sediments on the bottom. The absence of burrowing forms in most localities is suggestive of very low oxygen level in the sediment pore spaces. However, the presence of benthic organisms in the section suggests that adequate oxygen for their existence was available at the sediment-water interface. The generally complete, undisturbed nature of deposited layers with little or no evidence of erosion by bottom currents is further evidence for low oxygen levels (Schäfer, 1972).

Salinity varied locally in the basin depending on a number of conditions. To the south, brackish and some freshwater conditions existed near the shore of the Central Montana Trough embayment. To the east, brackish and freshwater environments predominated (Maughan, 1984). The presence of terrestrial plant parts in the south suggests these areas were not a great distance removed from the Bear Gulch Basin. The Mediterranean basin type circulation pattern implies stratification of salinity levels with higher salinity water flowing seaward from the bottom of the basin which is, in turn, overlain by more normal marine surface water entering the basin. This model is consistent with the marine character of the nektonic fauna and the absence of some expected normal marine benthos.

The Bear Gulch Limestone Beds formed in a shallow tropical basin with restricted, Mediterranean type water circulation. The basin was connected to the Central Montana Trough somewhere north of Potter's Creek Dome. Algal and bacterial mats surrounding the basin precipitated $CaCO_3$ in the form of micrite which was distributed by low energy currents entering the basin. Occasional, possibly seasonal, pulses of clastics reached the basin from rivers and streams prograding from the south and east. Water in the basin was sufficiently oxygenated to support plankton, fish and nektonic shrimp. Bottom conditions were influenced by elevated salinities and anaerobic sediment pore spaces.

Sedimentological and fossil evidence permits the characterization of a vital-pantostrate biocoenosis in the sense of Schäfer (1972). This biocoenosis is characterized by: 1, the presence of a limited benthic community; 2, a taphocoenosis of nektonic, benthic, and planktonic forms; 3, complete beds only occasionally disrupted or penetrated by benthos; 4, common coprolites and fossils; 5, small sediment grain size; 6, pore water low in O_2; 7, large number of well-preserved, more-or-less complete fossils; 8, material record of biofacies complete throughout the record; and 9, low perturbation in an off-shore, or sometimes near-shore, sublittoral zone.

SUMMARY AND CONCLUSIONS

Schram and Horner (1978) made the original descriptions of Bear Gulch malacostracans. They described five new species and documented the presence of five other species or genera. Utilizing specimens discovered since 1978 and reexamining material collected earlier, redescriptions of seven species recognized to occur in the Bear Gulch malacostracan assemblage have been made. *Aenigmacaris cornigerum, Belotelson magister, Crangopsis eskdalensis, Dithyrocaris rolfei, Perimecturus rapax, Sairocaris centurion,* and *Tyrannophontes theridion* are recognized. *Bairdops beargulchensis* is considered to be a junior synonym of *Tyrannophontes theridion.* The recognition that *Sairocaris centurion* has a bivalved carapace renders the Order Hoplocostraca unnecessary and permits placement of the Sairocarididae in the Archaeostraca. *Anthracophausia* sp. and *Pseudotealliocaris* sp. are not reconsidered in this study. The uniformly poor and incomplete quality of specimens previously assigned to these taxa render the assignments tentative and no new material substantially improves this situation. Nothing more can be done with these until better material becomes available.

The taxonomic composition of the malacostracan assemblage found in the Bear Gulch Limestone Beds is similar to the Glencartholm Volcanic Bed fauna (Visean) in Scotland and the Mazon Creek Essex fauna (Westphalian) in Illinois. Similarities, especially at the generic and family levels, to these faunas fit the pattern of a Carboniferous, near-shore, marine malacostracan assemblage as discussed in Schram and Horner (1978) and Schram (1979*a,* 1979*e,* 1981).

The near-shore marine nature of this chronofauna (in the sense of Olsen, 1966) provides an initial basis for environmental interpretations of the Bear Gulch Limestone Beds. The presence of nektonic and benthic malacostracans implies that conditions in the water column and at the sediment-water interface were conducive to animal life in at least part of the basin. The quality of preservation of arthropods and the preservation of bedding laminae suggest rapid sedimentation rates and absence of organic activity in the sediment. Arthropods are found throughout the section in the limestones of the Bear Gulch Member except at the very top of the section where shallowing produced brackish and supratidal conditions (Williams, 1981). Distribution of arthropod specimens around Potter's Creek Dome is not uniform. Specimens appear to be concentrated at three collection sites, 24, 28, and 51 (see Fig. 2). This distribution is interpreted to represent a patchy distribution of sites suitable for malacostracan occupation, although selective preservation may also be a factor in controlling distribution. As a result of the conditions outlined above, it appears the museum specimens of this fossil arthropod fauna have little more to offer to detailed study of the stratigraphy and sedimentology of their basin of deposition beyond the level presented in this paper.

ACKNOWLEDGMENTS

Dr. Richard Lund provided the opportunity for this study by bringing the project to the attention of Feldmann and supporting Factor while he spent time in the field with Lund's work crew in the summer of 1983. Tom Stanley, Loren Babcock, Larry Wiedman, and others spent time discussing much of the material presented in this paper. The curators of invertebrate fossils at the Carnegie Museum of Natural History generously loaned the specimens studied. Dr. Frederick Schram, San Diego Museum of Natural History volunteered specimens for our study and graciously commented on some of our systematic conclusions. Drs. Murray Copeland and Richard Lund reviewed the final manuscript. Finally, Dr. John Carter, Carnegie Museum, provided invaluable service in locating material in the collections and making that material available for study. Our sincere thanks to these gentlemen. Contribution 265, Department of Geology, Kent State University, Kent, Ohio 44242.

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A NEW LOOK AT *EUGASTERELLA LOGANI* (HALL, 1868) (STELLEROIDEA: OPHIUROIDEA) FROM THE MIDDLE DEVONIAN OF NEW YORK STATE

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Abstract

The Middle Devonian protasterid ophiuroid *Eugasterella logani* (Hall) is redescribed and illustrated from four newly acquired specimens collected from the Moscow Formation, Hamilton Group of Hamilton County, New York, consisting of molds of the oral sides of two individual animals, and molds of the oral and aboral sides of a single, large adult. Because Hall's type specimen showed only the oral aspect, this is the first record of the important aboral aspect of this species. The generic name *Eugasterella* was synonymized with *Protaster* Forbes in the Treatise on Invertebrate Paleontology, but is here reinstated because of significant differences in ossicle morphology with other recognized genera of Paleozoic ophiuroids. The dorsal longitudinal muscle scars of *Eugasterella* are much larger and deeper than those of *Protaster,* indicating a closer affinity with the related genus *Protasterina* Ulrich.

Introduction

James Hall (1868) described a new genus and species of Paleozoic ophiuroid, *Eugaster logani,* on the basis of a single specimen presenting the oral surface view. This fossil, from the Middle Devonian Hamilton Group of Madison County, New York, is fairly well preserved, but Hall's illustrations are highly stylized and don't do justice to the complexity of the ossicle morphology. Schuchert (1914), recognizing that the name *Eugaster* was preoccupied by a beetle, changed the generic

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designation to *Eugasterella.* Ruedemann (1916) attempted to provide more information on *Eugasterella* by illustrating details of the mouth frame, ambulacrals, and adambulacrals. It is unfortunate that he used drawings rather than photographs (as he did with many of the other stellaroids in the paper), because his illustrations are even more stylized than Hall's. Spencer (1934) synonymized Hall's genus and species with the Silurian ophiuroid *Protaster sedgwickii* Forbes, 1849, based on Hall's and Ruedemann's papers and a plasticine cast of the holotype. Kesling (1969) reinstated *Eugasterella* to its former status on the basis of a newly described species, *E. thorni,* from the Middle Devonian Arkona Shale of Ontario. As considered here, however, *E. thorni* is not referred to *Eugasterella* because of differences in general ossicle morphology between this species and Hall's type species.

The specimens of *E. logani* used as the basis for this study were collected by Robert M. Linsley, Colgate University, from the Moscow Formation in the Chenango Valley (Madison County) of New York. They include slabs of argillaceous siltstone containing molds of the oral and aboral sides of three separate animals. Two of the slabs contain the oral and aboral sides of a single, well-preserved adult, one slab holds the oral side of a single, well-preserved juvenile, and a fourth slab contains the oral side of a single, poorly-preserved juvenile. All known specimens of the species, with the exception of the holotype, are reposited in the Carnegie Museum of Natural History (CM), Pittsburgh, Pennsylvania. The holotype is at the New York State Museum (NYSM) in Albany, New York.

GEOLOGIC SETTING

The Devonian system of the north-central Appalachian Basin (New York and Pennsylvania) represents deposition under generally upwardly shallowing conditions. Rocks of the Lower Devonian and the lower half of the Middle Devonian consist mostly of relatively deep-water marine carbonates and detrital sandstones and mudstones. The upper half of the Middle Devonian and the Upper Devonian were deposited in marine, transitional, and continental environments dominated by the Catskill deltaic system, which Sevon and Woodrow (1981: 11) defined as "multiple contiguous deltas operating in the same sedimentary basin at approximately the same time." The clastic wedge deposited by the Catskill system comprises westwardly prograding terrigenous sediment, the thickest wedge of sediment of this sort in the Appalachian Basin. The laterally interfingering and upwardly coarsening rocks constitute a very complex series of flysch and molasse sequences that provide one of the most classic examples of the facies concept in North America.

Throughout much of Pennsylvania the upper Middle Devonian (Ca-

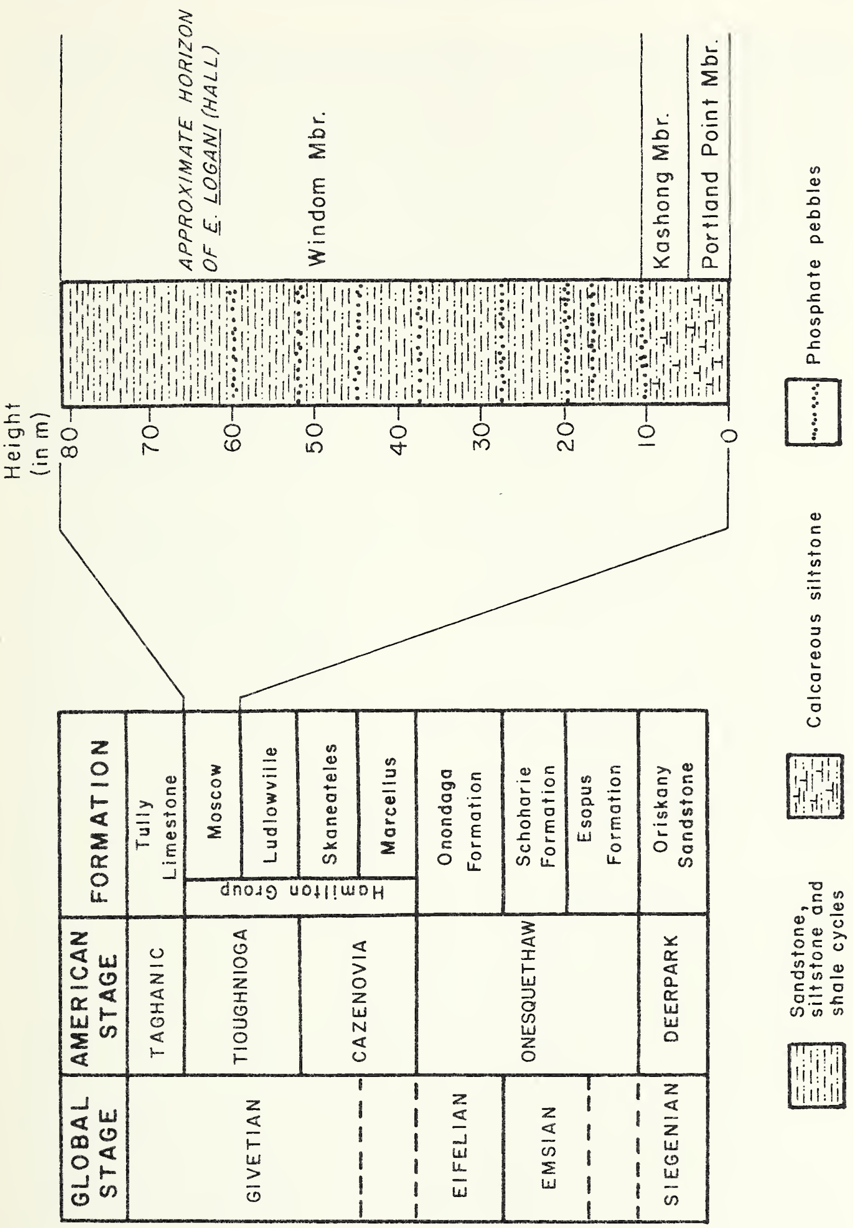


Fig. 1.—Generalized stratigraphic correlation of the late Early Devonian and Middle Devonian of central New York, showing the approximate horizon where *Eugasterella logani* was collected. The stratigraphic section of the Moscow Formation was modified from Zell, 1985.

zenovian and Tioughniogan stages) is dominated by the Mahantango Formation, a series of fine- to coarse-grained detrital rocks deposited close to the source area (what is now the Piedmont). Central New York state, however, was farther from these eroding uplands; the grain size of the rocks is generally smaller and the sediments are more marine influenced. This trend continues westward where, in western New York state, the number of beds of limestone and calcareous shales increases dramatically. These finer-grained clastics and carbonates of New York comprise the four formations of the Hamilton Group (Fig. 1). The Hamilton Group also thins toward the west, from 445 m in Madison County to 87 m at Lake Erie.

The youngest formation of the Hamilton Group, the Moscow Formation, consists of approximately 82 m of shales and siltstones in the Chenango Valley of central New York (Zell, 1985). Zell recognized three members of the Moscow Formation in this area (Fig. 1). The lower Portland Point and Kashong members consist of calcareous siltstones. The upper Windom Member is characterized by nine or more series of upwardly coarsening siltstone units. Each unit begins as a medium dark-gray, fine-grained siltstone deposited on an erosion surface, and grades upward to medium-gray, coarse-grained to sandy siltstone and very fine-grained sandstone. At least six of these units end with a thin bed or lens of coarse-grained siltstone or sandstone containing black phosphate pebbles. These pebbles have typically been interpreted as lag deposits marking the top of a regressive phase of eustatic sea level change (Zell, 1985).

The Windom Member contains numerous fossiliferous zones containing abundant epifaunal brachiopods (the dominant faunal element), bivalves, small corals (especially *Pleurodictyum*) and bryozoans, echinoderms, arthropods, and assorted gastropods and cephalopods. Zones of abundant fossils are normally separated by thick intervals of sparsely fossiliferous rocks, however. Epifaunal brachiopods and infaunal bivalves, mixed with some epiplanktonic brachiopods and bivalves, indicate the Windom was deposited in a variety of marine environments, from open marine shelf to poorly oxygenated lower slope (Grasso, 1978). The mud-bottom conditions in all these environments is suitable for burrowing and "mud-floating" organisms (such as epifaunal brachiopods and infaunal bivalves). Bryozoans probably supported themselves on such substrate by attaching the zoaria to shell fragments in the mud. Small tabulate corals, such as *Pleurodictyum,* tend to cement their coralla to shells or pebbles (Brett and Cottrell, 1981). The presence of *Eugasterella logani* and, potentially, other ophiuroids is not unexpected inasmuch as most of these animals prefer soft bottoms suitable for shallow burrows. Continued collecting in the Windom argillaceous siltstones is likely to result in the recovery of more specimens of *Eugasterella logani* and, possibly, the discovery of some new taxa.

SYSTEMATIC PALEONTOLOGY

Subclass Ophiuroidea Gray, 1840
Order Oegophiurida Matsumoto, 1915
Suborder Lysophiurina Gregory, 1896
Family Protasteridae Miller, 1889
Genus ***Eugasterella*** Schuchert, 1914

Eugaster Hall, 1868:293 (*non* Seville, 1839); Hall, 1870:332; Zittel, 1880:444; Ringueberg, 1886:8; Sturtz, 1886:151; Miller, 1889:244; Sturtz, 1893:20; Gregory, 1897: 1035.

Eugasterella Schuchert, 1914:19; Schuchert, 1915:237; Ruedemann, 1916, *non* Kesling, 1969:38.

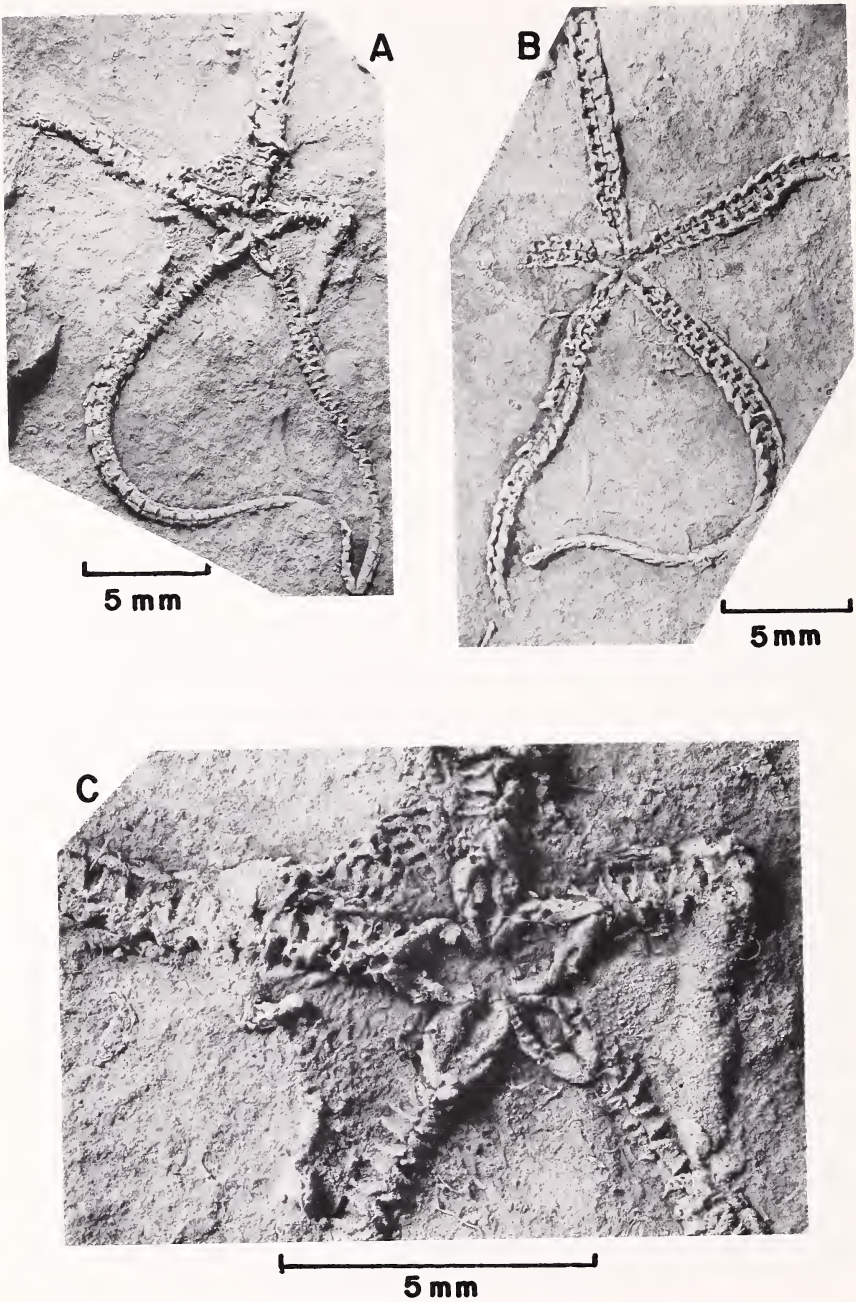
Protaster Forbes: Spencer, 1934:456 (in part); Spencer and Wright, 1966:U87 (in part).

Strataster Kesling and LeVasseur, 1971:317.

Diagnosis.—Protasterid ophiuroids having long, moderately wide, lanceolate or narrowly petaloid arms tapering gradually to blunt points. Disc subcircular to subpentangonal, with slightly to distinctly concave axils producing alate appearance at arm sides; covered with polygonal plates. Madreporite present. Mouth frame large; mouth-angle plates long and narrow; first ambulacrals large and stout, with well-developed grooves, apophyses, and pores on aboral side for directing water-vascular and neural systems. Ambulacrals with roughly boot-shaped oral surfaces; ambulacral groove slightly sinuous; aboral surfaces with wide, deep excavations for dorsal longitudinal muscles; podial basins large and well defined. Adambulacrals roughly ear-shaped, narrow, wrapped around sides of ambulacrals, with large nodes for attachment to ambulacral sides; spiniferous.

Remarks.—*Eugasterella* differs from most genera of the Protasteridae by having deeply excavated dorsal longitudinal muscle scars on the distal and proximal portions of the ambulacrals. Only *Protasterina* Ulrich, 1878, is similar to *Eugasterella* in this respect. *Eugasterella* and *Protasterina* differ in the size of the mouth-angle plates (those of *Eugasterella* are larger), the shape of the ambulacrals, the taper of the arms and the size of the longitudinal muscle scars. The muscle scars of *Protasterina* are so large that the aboral surface is triangular with only a narrow groove between the ridges of the muscle scars.

Spencer (1934) and Spencer and Wright (1966) diagnosed *Taeniaster* Billings, 1858, as having deeply excavated muscle scars. This was based primarily on one of three syntypes of *Palaeocoma spinosa* Billings, 1857, the type species of *Taeniaster.* Hotchkiss (1970), however, indicated that this one syntype specimen is unrelated to the other two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and tentatively placed it, with several other species, in the genus *Protasterina.* Hotchkiss concluded that *Taeniaster* had shallow muscle scars like *Protaster.*

Kesling and LeVasseur (1971) described the genus *Strataster* from the Mississippian Meadville Shale of Cuyahoga County, Ohio. *Strataster* and its type species, *S. ohioensis,* are based on thousands of specimens excellently preserved on bedding plane slabs. The generic diagnosis of *Strataster* is virtually indistinguishable from that of *Eugasterella* as given above. Both genera have large mouth frames, ambulacrals with trapezoidal aboral outlines and deeply excavated muscle scars, slightly sinuous ambulacral grooves, deep, well-defined podial basins, evenly tapering arms, and small, fairly conspicuous madreporites. In fact, there is so little difference between *Eugasterella* and *Strataster* that I must regard the genera as synonymous.

Eugasterella logani (Hall)

Figs. 2–7

Eugaster logani Hall, 1858:290, pl. 9, fig. 7, 8.
Eugasterella logani (Hall): Schuchert, 1914:19.
Protaster sedgwickii Forbes: Spencer, 1934:457 (in part).

Referred specimens.—The holotype, NYSM 409, is reposited at the New York State Museum, Albany, New York. Additional material, CM 34421A, 34421B, 34422, and 34423, are all in the Carnegie Museum of Natural History.

Locality.—All known specimens are from the Middle Devonian Hamilton Group of New York. NYSM 409 is from the area around Fenner, Madison County. The remainder of the material was collected from the Moscow Formation at the "Earlville Trilobite Quarry" in a government reforestation project, about 2 miles east of Earlville, Madison County.

Diagnosis.—Moderate-sized ophiuroids having long, lanceolate arms. Disc subpentagonal, slightly alate, covered by polygonal plates with raised ridges. Madreporite distinct, oval with apparent ridged and grooved surface. Mouth-angle plates long, narrow, and slightly curved. First ambulacrals large, stout, inclined to arm axis. Ambulacrals roughly boot-shaped orally, with wide podial basins and grooves at boot "ankle" for passage of water canal from ambulacral groove to tube feet; ambulacral surfaces trapezoidal aborally, with deep, wide spaces for attachment of dorsal-longitudinal muscles separated by fairly wide,

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Fig. 2.—Latex casts of *Eugasterella logani* (Hall), CM 34421. A, aboral view, CM 34421B; B, oral view, CM 34421A; C, enlarged section of aboral side, showing disc plates, granular integumen, and mouth frame with tori and pore-and-groove structures for water-radial system.

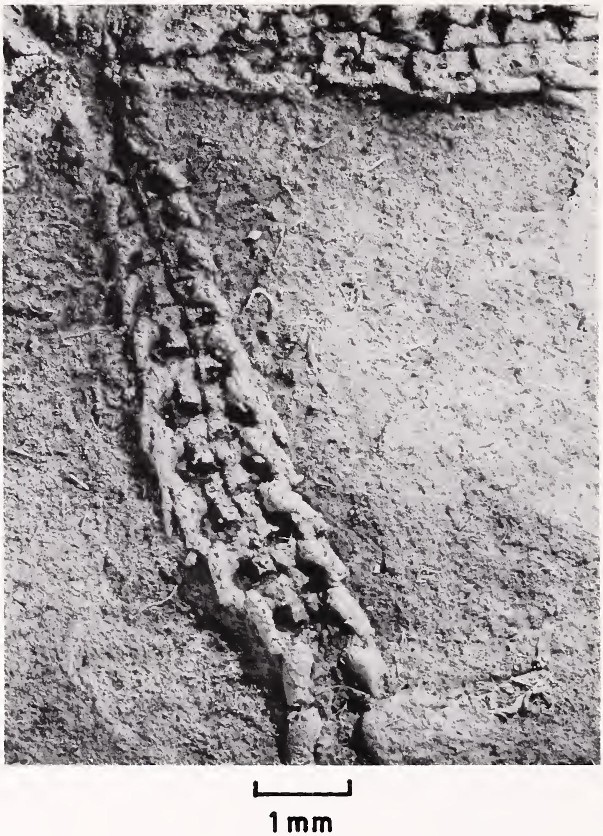

Fig. 3.—Latex cast of oral view of *Eugasterella logani* (Hall), CM 34421A, showing boot-shaped ambulacrals with relatively wide podial basins, and relationship of adambulacrals and spines.

central goove. Aborally, adambulacrals merely narrow, rectangular plates at side of ambulacral; orally, ear-shaped, and bearing vertical spines.

Description.—Moderate-sized ophiuroids with greater radius R (= center of mouth frame to arm tip) measuring 27 mm in the holotype, and lesser radius r (= center of mouth frame to center edge of axil) measuring 7 mm in the holotype. $R/r = 3.86$.

Disc: The oral and aboral surfaces of the disc are preserved in CM 34421A and 34421B respectively. The interradial margin of the disc is straight or slightly concave giving the disc an alate appearance at the arms. Aborally, the disc is composed of polygonal plates which tend

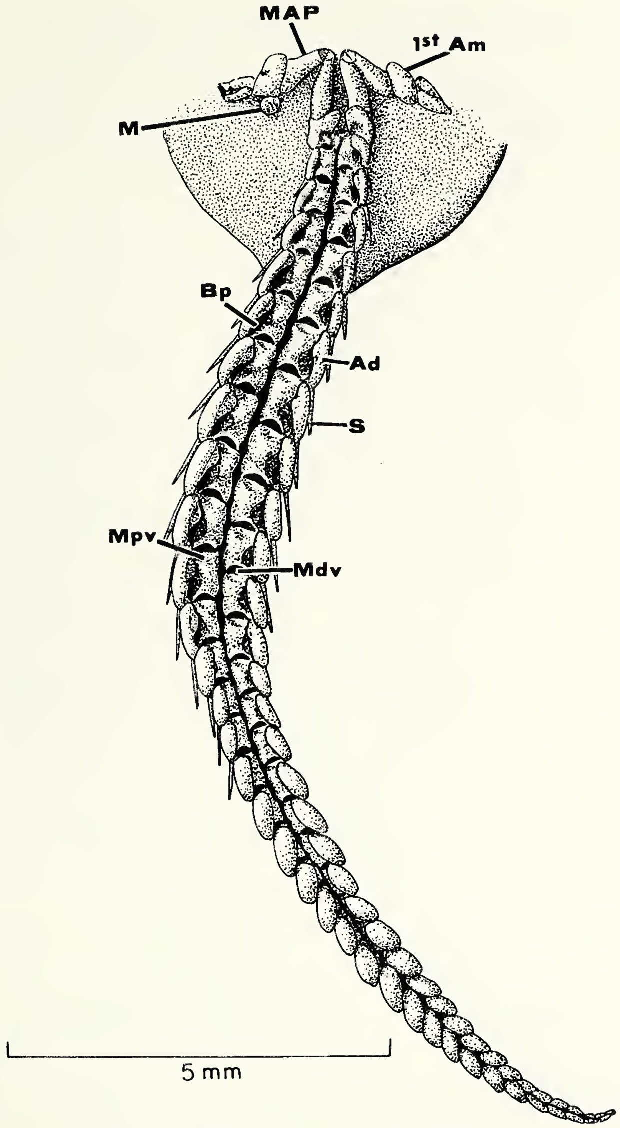

Fig. 4.—*Eugasterella logani* (Hall), reconstructed oral view of one ray. MAP—mouth-angle plate; 1st Am—first ambulacral; M—madreporite; Bp—podial basin; Ad—adambulacral; S—vertical spine; Mpv—proximal ventral muscle scar; Mdv—distal ventral muscle scar.

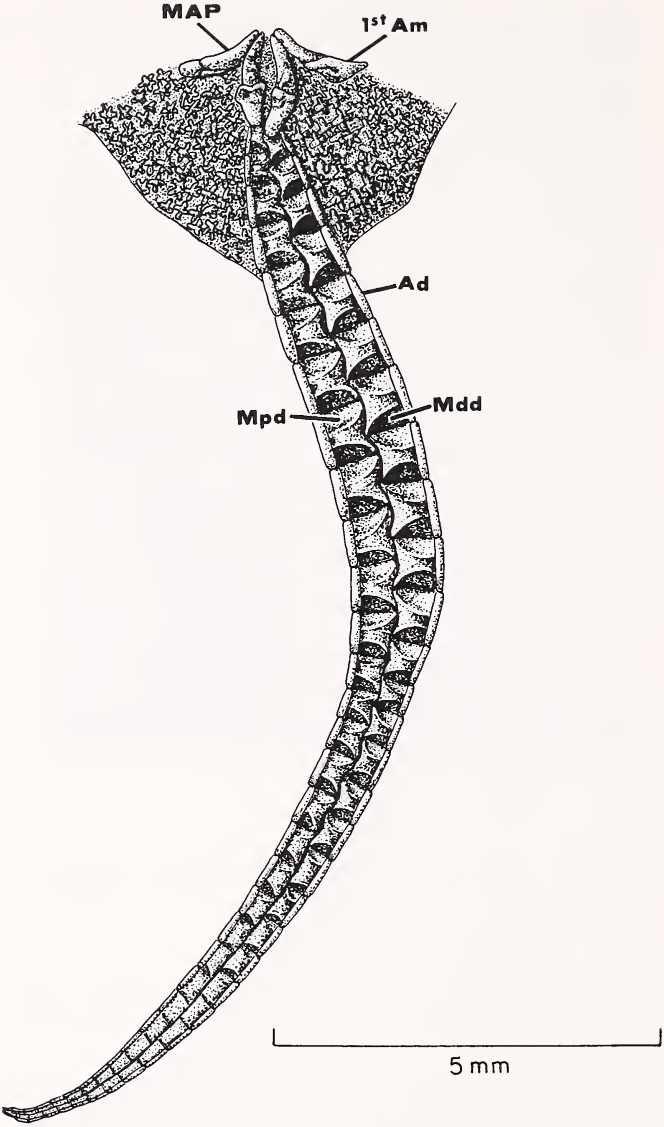

Fig. 5.—*Eugasterella logani* (Hall), reconstructed aboral view of one ray. MAP—mouth-angle plate; 1st Am—first ambulacral; Ad—adambulacral; Mpd—proximal dorsal muscle scar; Mdd–distal dorsal muscle scar.

to overlap one another. The surfaces of the plates have distinctly raised ridges which appear biaxial. The whole aboral surface was apparently covered with a thick integumen imbedded with fine granules. A portion of this integumen, as well as the underlying plates, can be seen in Fig. 2C. Orally, the plates covering the disc are not so prominent as in the aboral aspect, and the integumen does not appear to be so thick (Figs. 2B, 3).

Madreporite: The madreporite can be seen in the oral aspect in all the specimens showing the oral side (CM 34421A, 34422, and 34423). It is a small, convex, subcircular to elliptical plate with one or, possibly, two shallow grooves. The madreporite is situated on the disc in interray III/IV, adjacent to the distal portion of the first ambulacral of arm IV.

Mouth frame: The oral aspect of the mouth frame differs considerably from the oral aspect. Orally, the mouth-angle plates are parallelograms of moderately long and narrow aspect, forming wide V's where they join. The first ambulacrals are shorter and stouter with wide, somewhat circular or elliptical podial basins for the second tube feet occupying the distal portion of the ossicle. The podial basins for the first tube feet are not visible on any of the specimens examined. It is presumed that they lie facing inward toward the mouth cavity as in typical oegophiurids.

Aborally, the mouth frame is stronger and, in CM 34421B, shows better preservation than in the oral aspect. The mouth-angle plates are relatively long, narrow, and crescent-shaped. The first ambulacrals are stouter than the mouth-angle plates, as they are orally, but they are considerably longer on this side of the mouth frame. The mouth-angle plates have grooves for the nerve ring and water-radial canal, and with the apophyses which separate them (Figs. 2C, 6E). The pores for passage of the water-radial canal to the first and second tube feet are prominent within a groove on the proximal end of the first ambulacrals.

The tori are obscure, but can be seen in the mouth frame of the aboral aspect of CM 34421B (Figs. 2C, 6E) are completely displaced on all but one set of mouth-angle plates. The torus appears to be constructed of at least three closely set, subconical or subpyramidal denticles on a disc-like base. The middle denticle is slightly larger than the others.

Arms: The arms are narrowly petalloid or lanceolate, being widest in the proximal third of the ray. The arms taper uniformly from this area to the distal tips. The positioning of the ambulacral ossicles in each ray indicates lovenian symmetry, having the rays arranged AAB*AB in all specimens.

Ambulacrals: Orally, the ambulacral groove is slightly sinuous, dependent on the shape of the ambulacral halves (Figs. 2B, 3). The ambulacrals are stoutly rectangular overall and roughly boot-shaped on

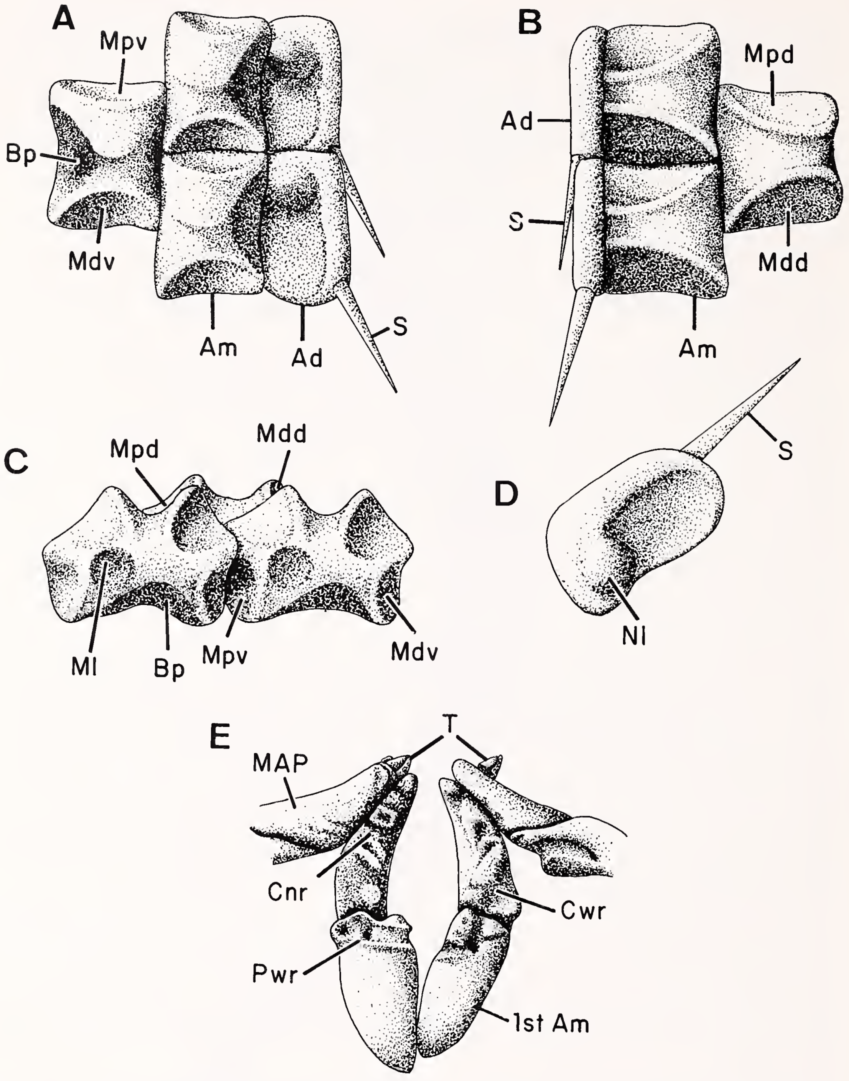

Fig. 6.—Ossicles of *Eugasterella logani* (Hall). A, relationship of ambulacrals and adambulacrals in oral view; B, relationship of ambulacrals and adambulacrals in aboral view; C, side view of ambulacrals; D, adambulacral and vertical spine; E, relationship of mouth-angle plates and first ambulacrals. Mpv—proximal ventral muscle scar; Bp—podial basin; Mdv—distal ventral muscle scar; Am—ambulacral; Ad—adambulacral; S—spine; N1—lateral node; Mpd—proximal dorsal muscle scar; Mdd—distal dorsal muscle scar; M1—lateral muscle scar; T—tori; MAP—mouth-angle plates; Cnr—nerve-ring canal; Cwr—water-radial canal; Pwr—water-radial pore; 1st Am—first ambulacral.

the oral surface, with the "sole" and "heel" in the proximal position (the back of the boot is adjacent to the ambulacral groove) (Fig. 6A). There is a wide, shallow groove on the "ankle" which apparently held the water-ring canal connecting the tube foot to the radial canal. This groove would also carry the nerve ring and pseudohemal canals. The podial basins are large and take up more than half of the outer side of the ambulacrals. Both ends of the ambulacrals show rather wide excavations for the insertion of the ventral longitudinal muscles. The ambulacrals articulate by a blunt peg-and-socket arrangement situated between the dorsal and ventral longitudinal muscle attachment areas.

Aborally, the ambulacrals are essentially rectangular (Fig. 6B). The grooved and ridged, saddle-shaped, aboral surface, however, gives these ossicles a superficial trapezoidal outline (Fig. 5). The non-parallel sides of the "trapezoid" are formed by ridges separating the dorsal longitudinal muscle attachment areas from the concave medial surface of the ambulacral. The dorsal muscle excavations are deep and wide. Where two ambulacrals articulate end to end, the depression formed by the combined proximal and distal muscle excavations is nearly as long as the ambulacral surface.

Adambulacrals: The adambulacrals are essentially ear-shaped in oral aspect (Fig. 6D). This shape is especially apparent where the adambulacrals are wrapped around the ambulacrals (Figs. 2B, 3, 7A). Otherwise they appear as simple, subrectangular plates, much longer than wide. The adambulacrals articulate with the ambulacrals by a peg-and-socket system situated on the proximal half of the plates (Fig. 6C, D). Vertical spines are present, although the exact number per adambulacral is questionable. CM 34421A appears to have only one stout, spike-like spine per plate (Fig. 3); the adambulacrals of CM 34422, however, have pustulate ventral edges similar to those of adambulacrals which bear numerous spines (Fig. 7A). None of the known specimens seems to have groove spines preserved, so it is unknown if the living animal had them.

The adambulacrals in aboral aspect are simple, narrowly rectangular plates abutting the outer sides of the ambulacrals (Fig. 6B). Because of this aspect, they may as easily be called laterals, in the same sense as in the Recent Ophiurida. Vertical spines cannot be seen aborally because they point orally (some can be seen attached to several of the adambulacrals in CM 34421A (Figs. 2B, 3, 6A).

Remarks.—There are no structural differences between Hall's specimen of "*Eugaster logani*" (NYSM 409) and the three specimens described and illustrated here. The holotype is not as well preserved as the new material, but the specifics of ossicle form and their interrelationships are unmistakably similar in all specimens examined.

Eugasterella logani differs from the Lower Mississippian *E. ohioensis*

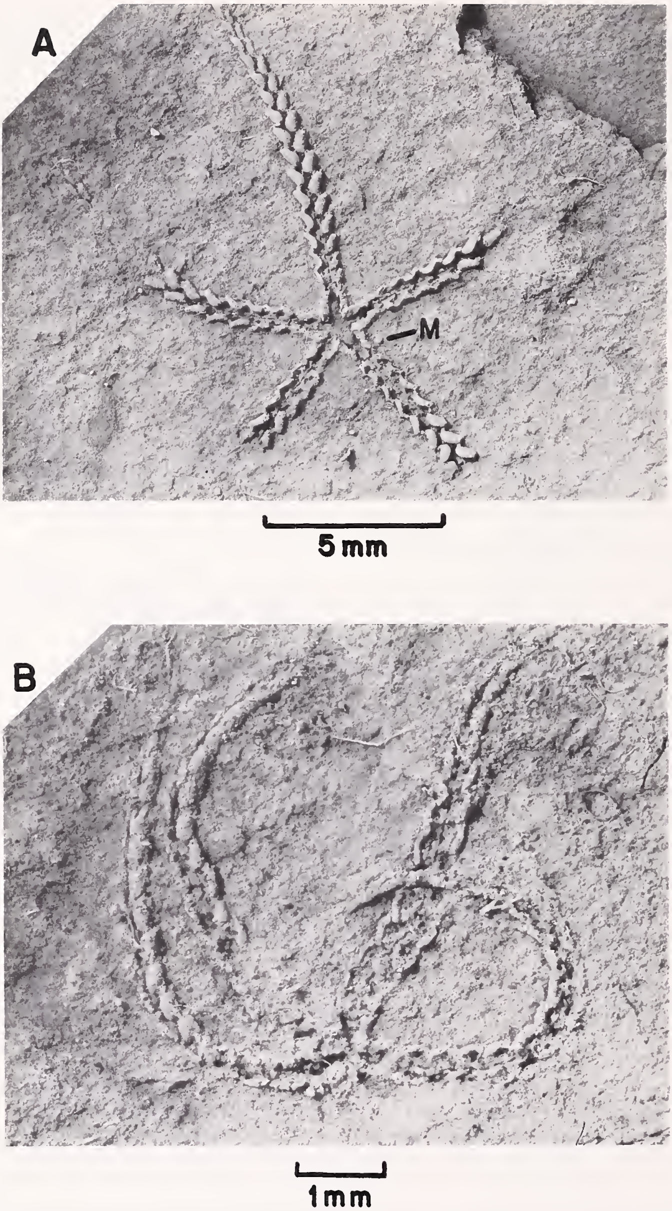

Fig. 7.—Latex casts of juvenile specimens of *Eugasterella logani* (Hall). A, CM 34422, M—madreporite; B, CM 34423.

Table 1.—*Measurements (in mm) of various attributes of* Eugasterella logani *(Hall), based on three specimens.*

Attribute	Specimen number		
	CM 34421	CM 34422	CM 34423
Disc diameter	6.8	4.3	2.7
Madreporite length	0.3	0.2	0.1
Madreporite width	0.2	0.1	0.1
Arm length	24.5	14.1	7.8
Proximal arm width	1.0	0.8	0.6
Medial arm width	1.5	1.0	0.8
Distal arm width	0.5	0.3	0.2

(Kesling and LeVasseur, 1971) in the form of the disc, the shape of the mouth frame and arms, the character of the tori, the articulation of the adambulacrals, and the number of vertical spines. The disc of *E. ohioensis* is more rounded, not concave interradially as in *E. logani.* The disc plates apparently are not ridged, and seem to be more irregular than those of Hall's species. The mouth-angle plates of the Mississippian form have better surface expression of the grooves and apophyses, although this may only be a matter of preservation. The first ambulacrals of *E. ohioensis* are more triangular in outline. The tori are better preserved and, therefore, are better known. They consist of flattened subelliptical plates bearing three spatulate denticles, as opposed to the more (seemingly) conical or pyramidal denticles of *E. logani.* Unlike *E. logani,* the arms of *E. ohioensis* are widest nearer the mouth frame, in the proximal quarter of the ray. The adambulacrals of the Mississippian species articulate with the ambulacrals by a long shelf-like peg-and-socket system. Each adambulacral bears two distinct vertical spines.

E. devonicus (Kesling, 1972) from the Silica Shale (Middle Devonian) of Ohio is also similar to *E. logani.* The greatest difference is the kind and number of spines exhibited by these two species. The Ohio species has four vertical spines attached to the distal edge of the adambulacral and an unknown number of supposed groove spines which are flattened and scapula-shaped. No better comparison of these two species can be made at this time because of the disarticulated nature of the two specimens of *E. devonicus.*

E. thorni Kesling, 1969 is probably incorrectly assigned to *Eugasterella.* None of the specimens used to describe and illustrate the species has the aboral side satisfactorily exposed. Integumen covers the proximal portion of the rays. Despite this, Kesling diagnosed the species (and genus) as lacking deep excavations for the dorsal longitudinal muscles. In addition, the mouth frame is short and stout, and the adambulacrals are more roundly rectangular than ear-shaped. This species is probably more closely allied with *Protaster* Forbes, than with *Eugasterella*.

Of the remaining species assigned by previous workers to *Eugaster* or *Eugasterella, E. aranea* Ruedemann (1916) is the type species of the genus *Mastigactis* Spencer, 1930, and *E. bicatenulatus* Ruedemann (1916) was reassigned to *Protaster* Forbes by Spencer (1934). *Eugaster concinna* Ringueberg, 1886, was determined by Schuchert (1915) not to belong to *Eugasterella*. I have not seen either the specimen described by Ringueberg or an illustration and can, therefore, add nothing to our knowledge of it.

Measurements.—Measurements are given in Table 1.

ACKNOWLEDGMENTS

I am indebted to Robert M. Linsley for finding and donating the specimens of *Eugasterella logani* described and illustrated in this paper. Paul Zell, University of Pittsburgh, spent some time discussing the stratigraphy and paleontology of the Moscow Formation in Madison County, and for that I am grateful. Comparative ophiuroid material was provided by the New York State Museum, Albany, the Carnegie Museum of Natural History, Pittsburgh, and the University of Michigan Museum of Paleontology, Ann Arbor. Daniel B. Blake, University of Illinois, and Robert V. Kesling, University of Michigan, acted as reviewers and their comments and criticisms have aided in significantly improving the quality of the paper. This paper is published with the permission of Arthur A. Socolow, Director of the Pennsylvania Geological Survey.

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THE LOWER MISSISSIPPIAN BRACHIOPOD GENUS *PUNCTOTHYRIS* HYDE IS NOT ENDOPUNCTATE

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Abstract

Reexamination of the type specimens of *Punctothyris argus* Hyde shows that the so-called punctae described by Hyde in his original description of the genus are molds of inner extensions of very small hollow papillae or spinules. These hollow "punctae" terminate within the secondary or fibrous shell layer and thus are not endopunctae. The genus *Punctothyris* is rediagnosed and assigned to a new reticulariacean family, the Gerkispiridae. *Spirifer schucherti* Rowley is redescribed and assigned to *Punctothyris* and two new species of this genus are described, *P. kenwoodensis* from the St. Joe Limestone of northeastern Oklahoma, and *P. inusitata* from the Chouteau Limestone of northeastern Missouri.

Introduction

In his monographic treatment of the invertebrate faunas of the Logan and associated formations of the Waverly Group of east-central Ohio, Jesse Hyde (1953:287–289) described an unusual and enigmatic genus of spiriferoid brachiopods to which he applied the name *Punctothyris*. His brief description follows: "Shell spiriferoid, punctate, with much reduced, but distinct dental lamellae and with no median septum." Because punctate spiriferids lacking a median septum are so unusual, it is not surprising that other workers have failed to cite this genus in the literature. Difficulty in recognizing the genus has been further compounded by the poor preservation of Hyde's types from the Logan

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Formation and the fact that Hyde failed to illustrate any specimens of his new genus with photographs.

Pitrat, in the Treatise on Invertebrate Paleontology (1965:H714), assigned *Punctothyris* to the punctate family Spiriferinidae with a query and the parenthetic caveat that Hyde's ". . . punctae may be merely spine bases, in which case *Punctothyris* should be reassigned to the Spiriferidae." Pitrat's suspicion concerning the nature of the "punctae" was well founded.

My original interest in this genus came about after I had successfully sectioned a silicified chert-filled specimen of *Spirifer schucherti* Rowley from the collections of the University of Illinois. Although very small and with somewhat different proportions than *P. argus* Hyde, it was very similar to that species externally and internally except in one important aspect—it was seemingly not punctate (although all other endopunctate silicified species in the white chert fauna gave some clear indication of punctae). This, taken with Pitrat's suspicion concerning the nature of Hyde's "punctae," prompted me to examine Hyde's type material. The discovery of two new species of this genus has provided additional incentive to rediagnose Hyde's misunderstood genus.

The abbreviations OSU, US, and CMNH refer to the Ohio State University, University of Illinois at Urbana-Champaign, and the Carnegie Museum of Natural History, respectively.

SYSTEMATIC PALEONTOLOGY

Order Spiriferida Waagen
Suborder Spiriferidina Waagen
Superfamily Reticulariacea Waagen
Family Gerkispiridae, new family

Diagnosis.—Entirely costate, ovate to transverse reticulariaceans with short hingeline and moderately to well developed fold-sulcus; pedicle valve with short thin dental adminicula, low thin flaring stegidial plates, fine denticles in the outer lamellar layer of the interarea, and commonly with low apical myophragm; brachial valve interior with short tabellae and small striate cardinal process; micro-ornament consists of very fine uniramous hollow papillae or spinules that originate in the fibrous secondary shell layer; shell substance impunctate.

Genera assigned.—*Gerkispira* Carter, 1983, and *Punctothyris* Hyde, 1953.

Stratigraphic range.—Lower Mississippian (Tournaisian).

Remarks.—This new family is assigned to the Reticulariacea on the basis of well rounded lateral extremities, lack of true spiriferid denticulation (with taleolae in the secondary layer of the interarea of the pedicle valve), interior morphology, and micro-ornament of its constituent genera. The entirely costate macro-ornament separates this group from other reticulariacean families.

Genus ***Punctothyris*** Hyde, 1953

1953. *Punctothyris* Hyde, Bull. Ohio Geol. Surv., 51:287–289, pl. 36, figs. 1–11.
1965. *Punctothyris* Hyde: Pitrat, Treatise on Inv. Paleont., Part H, Brachiopoda, p. H714, fig. 582, 1.

Type species.—Punctothyris argus Hyde, 1953, from the Logan Formation, Byer Member, Sciotoville, Ohio.

Other species assigned.—Spirifer schucherti Rowley, 1900, from the Lower Burlington white chert at Louisiana, Missouri; *Punctothyris inusitata* new species, from the Couteau Limestone in Marion County, Missouri; and *Punctothyris kenwoodensis* new species, from the St. Joe Limestone of Mayes County, Oklahoma, are readily placed here. *Reticularia? subrotundata* Hall of Girty (1899:557–558, pl. 70, figs. 7a, b) from the Madison Limestone in Montana probably belongs in this genus or in *Gerkispira* Carter. Girty compared his specimen with a species found in the lower Burlington Limestone of Pike County, Missouri, possibly referring to *P. schucherti* (Rowley). Girty's specimen is clearly not assignable to *Spirifer subrotundus* Weller (=*S. subrotundatus* Hall).

Diagnosis.—Small ovate to transverse reticulariaceans with rounded lateral extremities in all growth stages and well delimited fold-sulcus; both valves with a moderate number of simple rounded costae on the flanks and one to several simple costae in the sulcus or on the fold; sulcus bounding costae prominent and giving rise to lateral sulcal costae, when present, and occasionally to the nearest costae on the flanks; micro-ornament consisting of numerous fine hollow erect or semi-erect spinules or papillae that terminate within the fibrous secondary shell layer and fine growth lines; pedicle valve interior with slender short dental adminicula and short apical myophragm; brachial valve interior with very small cardinal process composed of a few longitudinal plates and short vertical tabellae; shell substance impunctate.

Comparisons.—The recently described genus *Gerkispira* Carter is similar to *Punctothyris* in most respects, but the latter can be readily differentiated by its less transverse outline, fewer costae, and well differentiated fold-sulcus. In micro-ornament and internal morphology the two genera are almost identical.

Few other spiriferacean or reticulariacean genera are closely similar to those of the Gerkispiridae. The Middle Devonian genus *Elythyna* Rzhonsnitskaya, 1952, possesses slightly rounded lateral extremities, low wide simple plications on the flanks, and has a micro-ornament consisting of fine long spinules or papillae. Internally the pedicle valve is similar to *Punctothyris* but the brachial valve interior presumably lacks tabellae. *Elythyna* is much larger and has more weakly impressed macro-ornament than *Punctothyris.*

Oiosia Cooper and Dutro, 1982, from the Box Member of the Percha Formation of New Mexico (Late Famennian), is similar in size, outline, internal morphology and micro-ornament to *Punctothyris.* It differs in having a non-costate fold-sulcus and the ribs on the flanks are weakly or sometimes obscurely developed.

The ribbing on the fold-sulcus of *Punctothyris schucherti* and *P. argus* is not strongly developed, consisting of a single medial costa in the sulcus of *P. schucherti* and one to four obscure costae in the sulcus of *P. argus.* It is possible that *Punctothyris* and the Gerkispiridae arose from a progenitor with a non-costate fold-sulcus such as *Oiosia.*

Punctothyris argus Hyde, 1953
Figs. 1A–M; 2A–C

1953. *Punctothyris argus* Hyde, Bull. Ohio Geol. Surv., 51:288–289, pl. 36, figs. 1–11.
1965. *Punctothyris argus* Hyde: Pitrat, Treatise on Invert. Paleont., Part H, Brachiopoda, p. H714, fig. 582, 1.

Holotype.—OSU 12656 (H-540, incorrectly cited as H-500 in Hyde: 289). Collected by Hyde from the Byer Member of the Logan Formation at Sciotoville, Scioto County, Ohio.

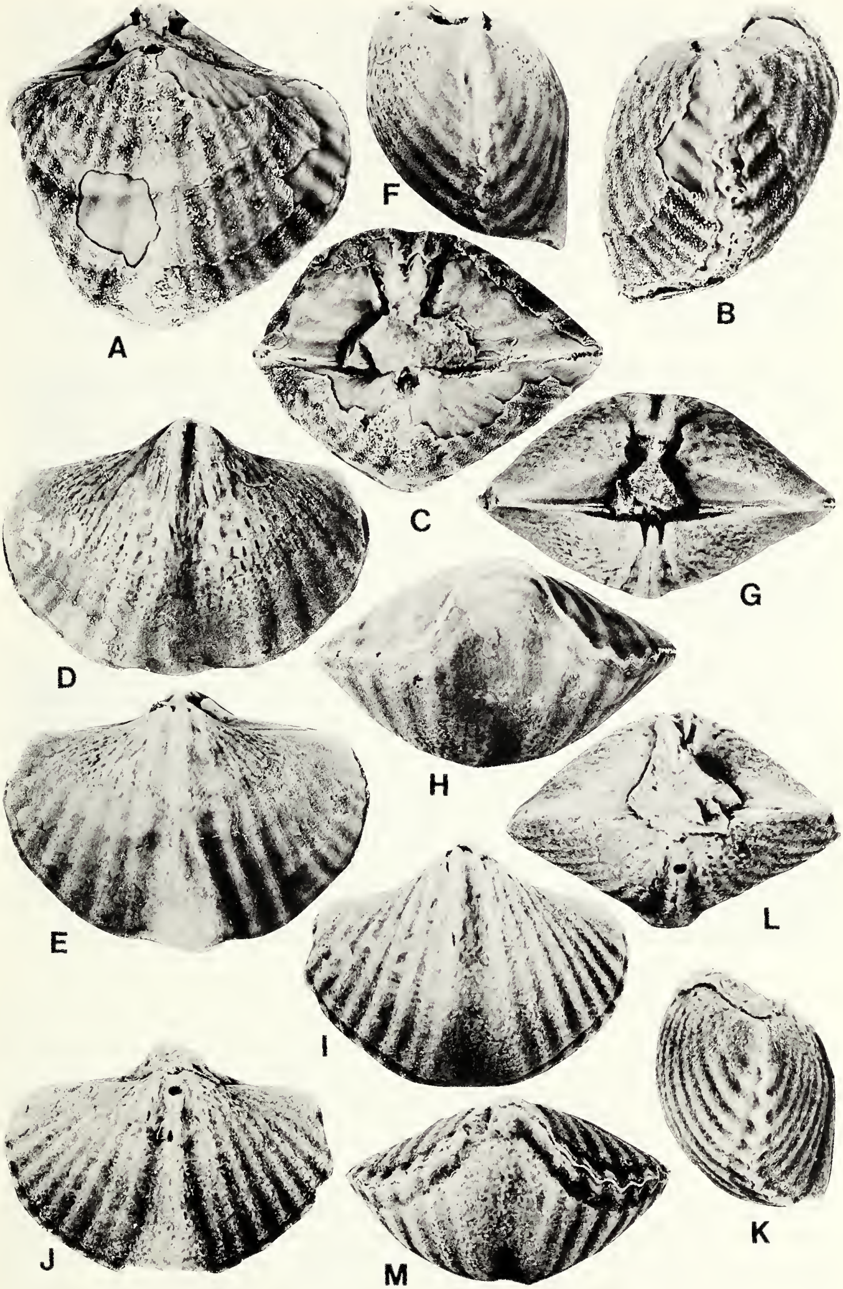
Paratypes.—OSU 12656 (H-542, 543, 545); the following designated paratypes are apparently lost: H-502, 504, 505, 507, 541, 544, and 546. All paratypes are from the same collection as the holotype.

Description.—Medium size for the family, subequally biconvex, with transversely subovate to subquadrate outline; maximum width attained slightly anterior to midlength; lateral profile sublenticular; lateral extremities rounded in all growth stages; anterior commissure uniplicate; fold and sulcus rather narrow, moderately developed, well defined; ornament consisting of 8 to 10 rounded costae on the flanks and one to four obscure costae in the sulcus; only those costae adjacent to the fold-sulcus may occasionally bifurcate; intercostal furrows of about the same amplitude and breadth as the costae; almost entire surface covered with tiny longitudinally ovate hollow papillae or spinules, roughly arranged in quincunx, which terminate within the secondary fibrous layer, leaving no indication of penetrating to the shell interior (see Figure 1A); shell substance impunctate.

Pedicle valve moderately inflated, slightly thicker than opposite valve; maximum

→

Fig. 1.—*Punctothyris argus* Hyde. A–C, dorsal, lateral and posterior views of a large incomplete paratype, O.S.U. 12656 (H-545), note the smooth internal mold in areas where the secondary shell layer is missing; D–H, ventral, dorsal, lateral, posterior, and anterior views of the holotype, a steinkern, O.S.U. 12656 (H-540); I–M, ventral, dorsal, lateral, posterior, and anterior views of a paratype, O.S.U. 12656 (H-543), a steinkern with small amounts of shell material preserved at the two beaks; all ×3.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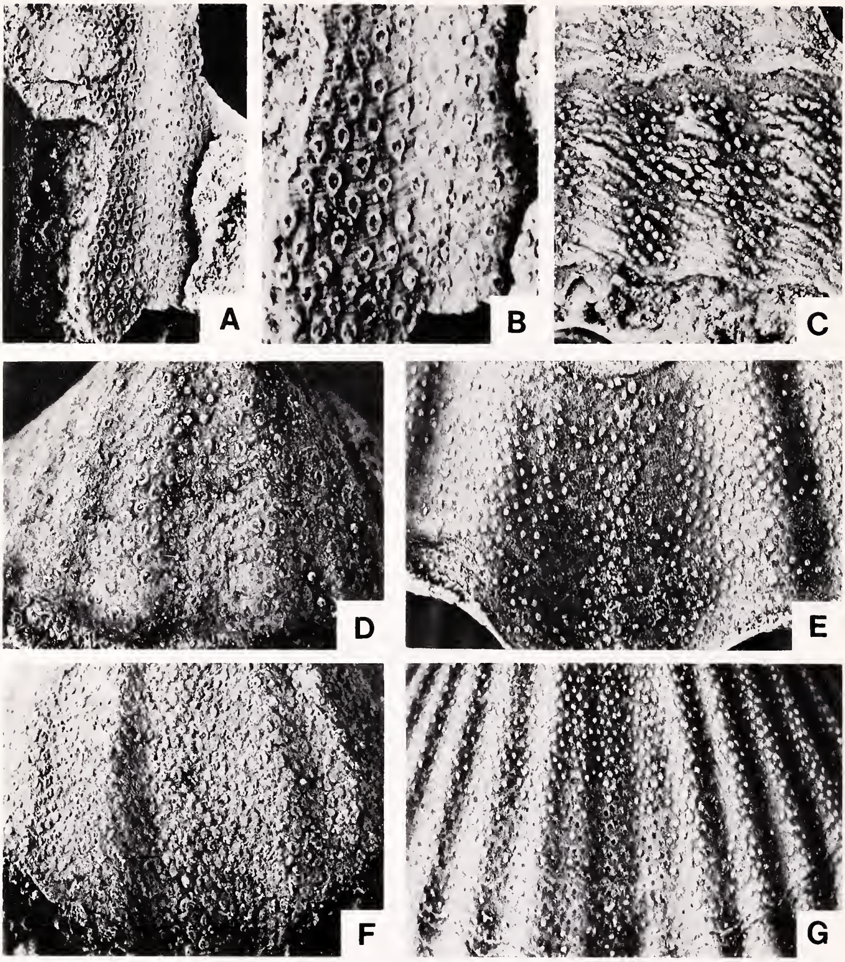

Fig. 2.—Micro-ornament of the genus *Punctothyris.* A–C, *Punctothyris argus* Hyde; A, B, enlargements of the hollow spinule bases of paratype O.S.U. 12656 (H-542), ×10 and ×22, respectively; C, enlargement of molds of the hollow spinule bases on paratype O.S.U. 12656 (H-545), ×10. D, F, *Punctothyris schucherti* (Rowley); D, paralectotype Univ. Illinois RX-25A, a pedicle valve; F, a pedicle valve, CMNH 34497; both ×10. E, *Punctothyris kenwoodensis,* new species, paratype CMNH 34492, ×10. G, *Punctothyris inusitata,* new species, holotype CMNH 34495, ×10.

thickness attained in umbonal region posterior to midlength; umbonal region moderately inflated; flanks moderately convex medially, sloping evenly to lateral margins; cardinal extremities slightly compressed, rounded; beak small, narrow, slightly incurved; internal molds suggest that interarea was low, acutely triangular, apsacline; no indication of denticulation preserved on types; delthyrium about as wide as high, definitive indication of stegidial plates lacking in types; sulcus originating in beak, remaining moderately narrow, shallow, and rounded throughout; sulcus moderately well delimited from flanks; sulcus-bounding costae uniform throughout, occasionally giving rise to lateral sulcal costae; costae near cardinal extremities very faint; sulcal costae often faint, hightly variable in development.

Pedicle valve interior with short stout diverging dental adminicula and a low rounded median ridge or myophgram in the umbonal region; muscle field moderately impressed; ovarian pits well developed anterolaterally to the muscle field in the holotype.

Brachial valve moderately convex but thinner than the pedicle valve, with the maximum thickness attained near midlength of the valve; umbonal region moderately swollen, not projecting much posterior to the hingeline; flanks curving evenly to the lateral margins, cardinal extremities slightly compressed; beak small, incurved; dorsal interarea low, slightly concave, anacline; fold originating in the umbonal region, remaining low until anterior to midlength, then rising moderately to form lateral profile nearly parallel to the lateral margin; fold well delimited throughout by fold bounding furrows which are more deeply incised than those on the flanks; ornament similar to that of the opposite valve.

Brachial valve interior with a very small striate cardinal process composed of five or six vertical plates; inner socket ridges fused with the crural bases, forming short stout vertical tabellae; adductor impressions obscure but a very thin low myophragm extends from near the base of the cardinal process to about midlength; brachidial details unknown.

Hyde (1953:289) presented accurate measurements of the holotype and the three best preserved paratypes.

Distinguishing characters.—This species is characterized by its transverse outline with 8 to 10 costae on the flanks and one to four costae in the sulcus.

Comparisons.—The other three species assigned to this genus can be differentiated in the following manner. *Punctothyris schucherti* (Rowley) is much smaller with a subovate outline and only six lateral costae and one in the sulcus. *Punctothyris kenwoodensis,* new species, is about the same size as *P. argus* but has an ovate outline, a more inflated profile in large specimens, 8 to 11 lateral costae and zero to three costae in the sulcus. *Punctothyris inusitata,* new species, is much smaller, has a less transverse outline, 13 lateral costae and three to five sulcal costae.

Occurrence and abundance.—Hyde's types are the only collection of this species of which I am aware. His specimens came from the Byer Member of the Logan Formation near Sciotoville (Sciotodale), Scioto County, Ohio. The age of the Logan Formation is in dispute. Although Stockdale (1939:228) indirectly suggested that the Logan Formation was of Keokuk age, Rodriguez (in Root et al., 1961:56) proposed that the Logan was no younger than Burlington in age. Manger (1971:34) concluded that the Logan was Kinderhookian in age, based on his study of the ammonoid fauna. Discovery of conodonts in the Rushville Formation by Thompson et al. (1971:704–711) conclusively limits the Logan to being no younger than Fern Glen or Early Osagian. Although the underlying Cuyahoga brachiopods appear to have strong Late Kin-

Table 1.—*Measurements (mm) of the type specimens of* Punctothyris schucherti.

Number	Length	Width	Thickness
U.I.RX 25D	8.7	9.5	6.3+
U.I.RX 25	7.9	7.6+	5.0+
U.I.RX 25A	5.3	6.9	3.2
U.I.RX 25C	5.2+	5.2+	3.5+
U.I.RX 25B	3.8+	3.8+	2.3+

derhookian affinities, the Logan brachiopods are too endemic to be of much biostratigraphic value.

Punctothyris schucherti (Rowley, 1900)
Figs. 2D, F; 3H–N; 4

1900. *Spirifer schucherti* Rowley, American Geologist, 25:261–262, pl. 5, figs. 15–17, 59.
1914. *Spiriferella? schucherti* (Rowley): Weller, Monogr. Illinois Geol. Surv., 1:416–418, pl. 35, figs. 59–63.
1941. *Spiriferella? schucherti* (Rowley): Butts, Bull. Virginia Geol. Surv., 52:220, pl. 124, figs. 25, 26.

Lectotype (designated herein).—University of Illinois RX-25D; from the lower Burlington white chert at Louisiana, Pike County, Missouri. This is the largest and by far the best preserved of Rowley's syntypes and is probably the same specimen figured by Weller (1914:pl. 35, figs. 59–63).

Paralectotypes.—University of Illinois RX 25, 25A, 25B, 25C. All are from the same collection as the lectotype.

Distinguishing characters.—This species can be differentiated by its small size (Table 1), subovate outline, six lateral costae, and a single median costa in the sulcus.

Comparisons.—The distinctions between this species and the type species of the genus, *P. argus,* are pointed out in the above discussion of that species. *P. kenwoodensis,* new species, from the St. Joe Limestone of Oklahoma, is of about the same age as *P. schucherti.* It differs in being much larger with a more ovate outline, a more inflated lateral profile, 8 to 11 lateral costae, and commonly three costae in the sulcus. In addition, *P. kenwoodensis* has a much broader umbonal region, less compressed cardinal extremities, and a more inflated brachial valve. In specimens of comparable size, the broad ventral umbo and slightly more numerous ribs on the flanks and often in the sulcus and more evenly rounded outline of *P. kenwoodensis* allow discrimination of the two species. *P. inusitata,* new species, from the Chouteau Limestone of northeastern Missouri, is slightly larger than *P. schucherti* but is similar in outline and development of a narrow ventral umbo. How-

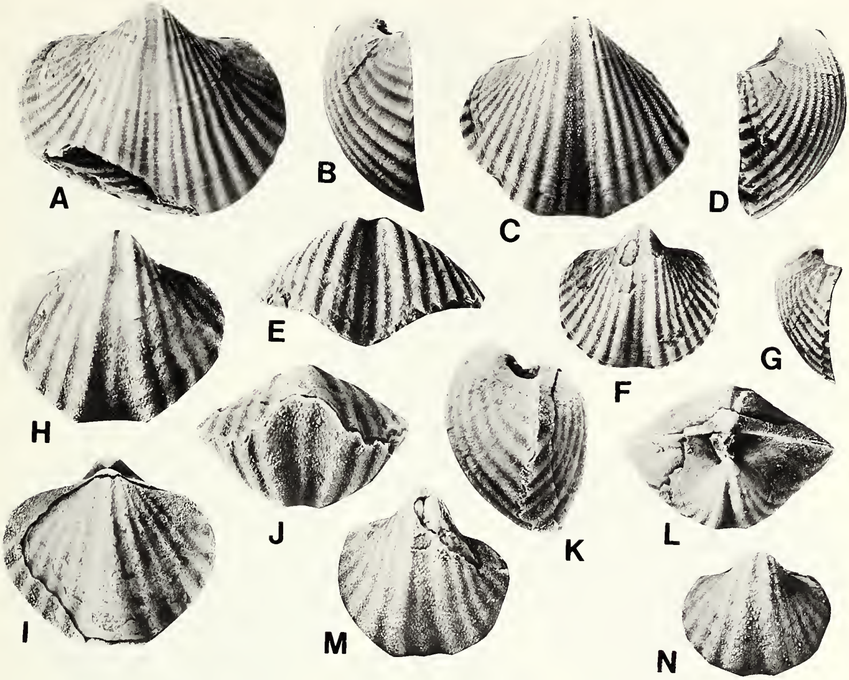

Fig. 3.—A–G, *Punctothyris inusitata,* new species; A, B, ventral and lateral views of a large pedicle valve paratype, CMNH 34494; C–E, ventral, lateral, and anterior views of a medium pedicle valve, the holotype, CMNH 34495; F, G, ventral and lateral views of a small pedicle valve paratype, CMNH 34496; all ×3.

H–N, *Punctothyris schucherti* (Rowley); H–L, ventral, dorsal, anterior, lateral, and posterior views of the lectotype, Univ. Illinois RX-25D; M, a small elongate pedicle valve, CMNH 34497; N, a small pedicle valve paralectotype, Univ. Illinois RX-25A; all ×3.

ever, *P. inusitata* can be readily differentiated by its more numerous costae on both the flanks and sulcus.

Remarks.—Although Weller's excellent description of the exterior morphology of this species scarcely needs repeating some additional information concerning the nature of the ornament, shell structure, and internal morphology has come to light. Weller (1914:417) was incorrect in stating that *P. schucherti* is punctate. Although he did not describe the structures he interpreted as punctae, one may assume he was referring to the bases of the hollow spinules or papillae that characterize this genus and which extend into the secondary layer of the shell.

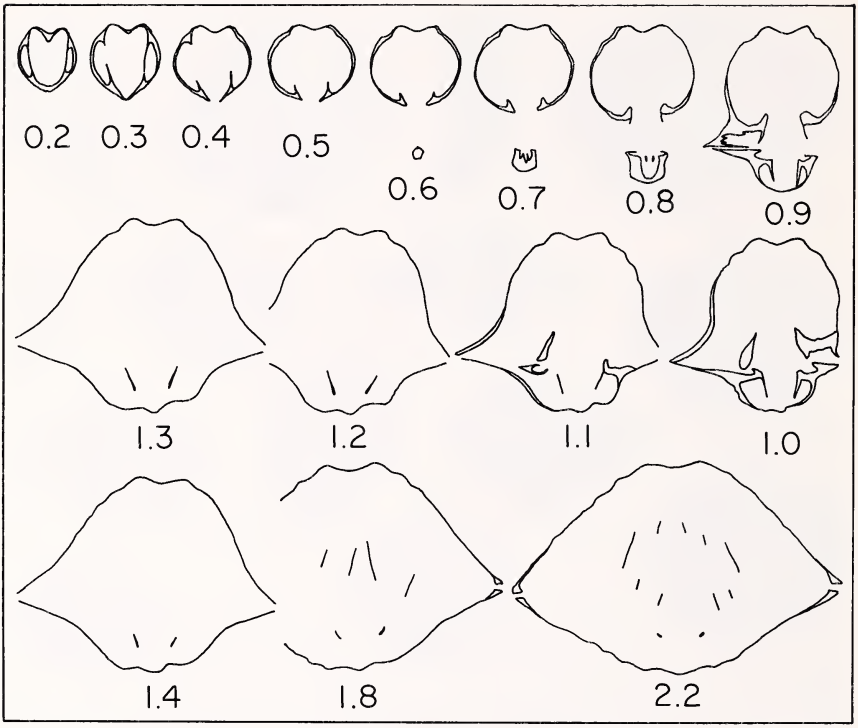

Fig. 4.—Transverse serial sections of *Punctothyris schucherti* (Rowley). An R. R. Rowley Collection specimen from the white chert of the Lower Burlington Limestone at Louisiana, Pike County, Missouri, Univ. Illinois X-6352, ×6. Section numbers refer to distance in millimeters from the ventral beak.

The interior morphology of this species can be ascertained from transverse serial sections as seen in Fig. 4. The interior of the pedicle valve possesses very short thin dental adminicula. A short low myophragm is confined to the beak region. Also note the thin outwardly flaring stegidial plates that appear 0.8 mm from the posterior tip of the beak. In the brachial valve, the cardinal process is exceptionally small

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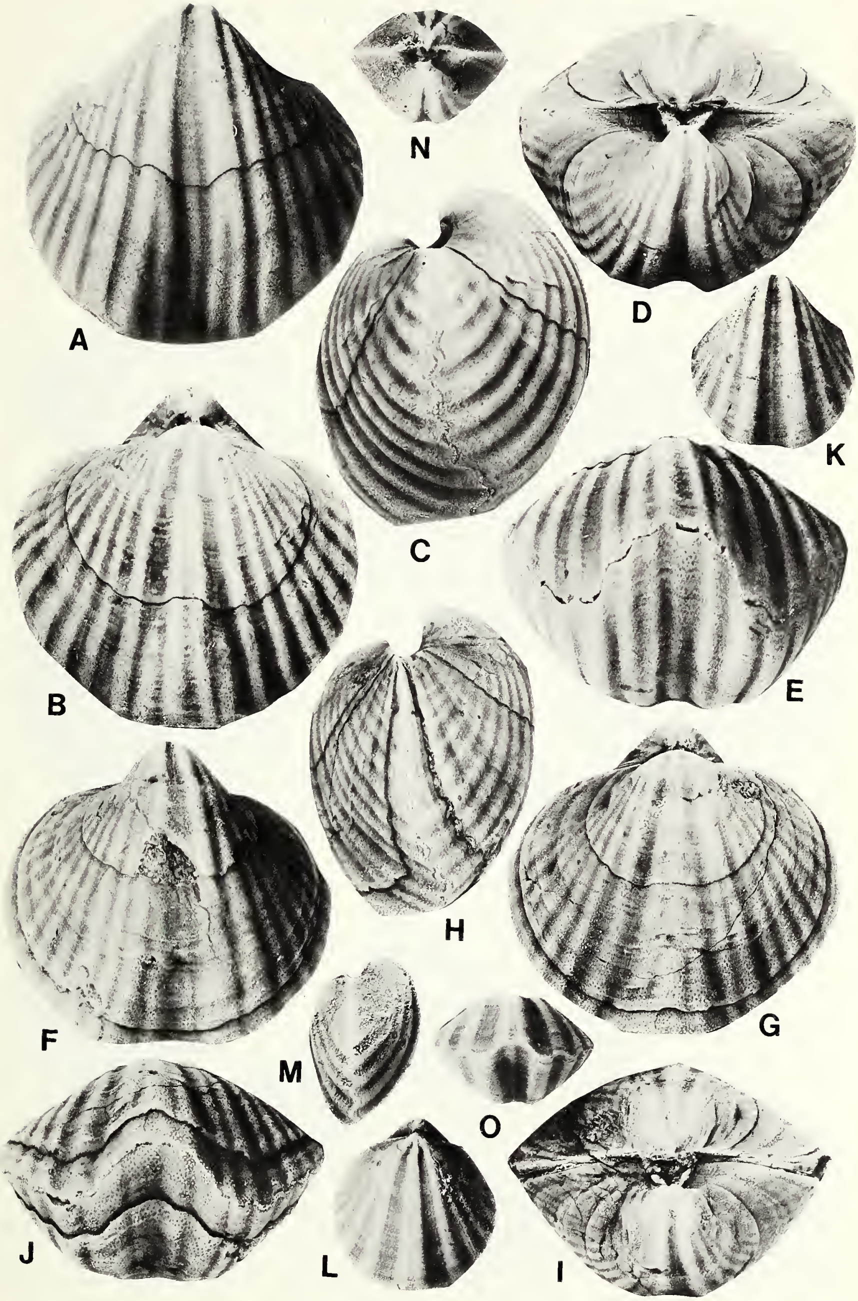
Fig. 5.—*Punctothyris kenwoodensis,* new species; part of a growth series of seven specimens (also see Fig. 6); A–E, ventral, dorsal, lateral, posterior, and anterior views of the holotype, CMNH 34485; F–J, ventral, dorsal, lateral, posterior, and anterior views of a large paratype, CMNH 34486; K–O, ventral, dorsal, lateral, posterior, and anterior views of a small paratype, CMNH 34490; all ×3.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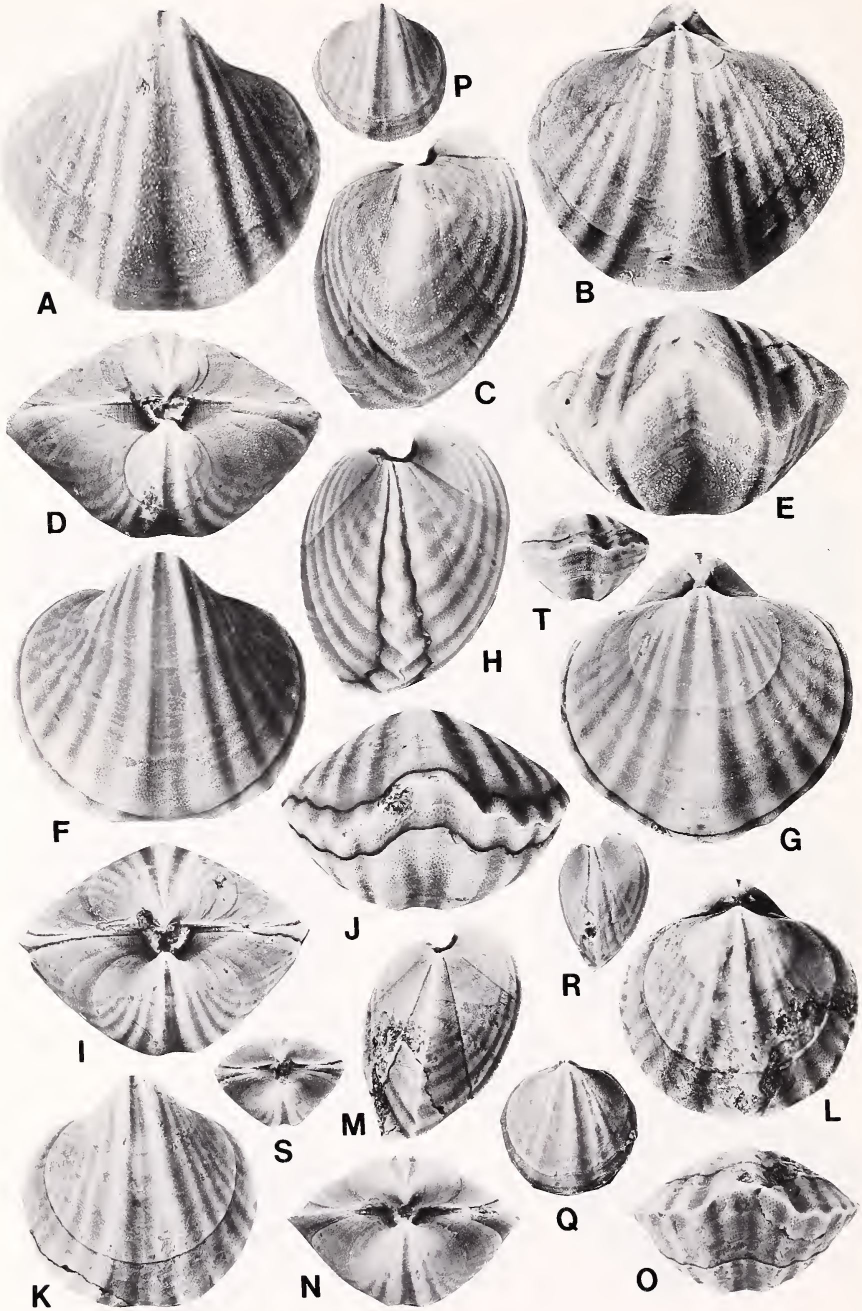
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Table 2.—*Measurements in millimeters of the types of* Punctothyris kenwoodensis.

CHMN number	Length	Width	Thickness
34485	15.7	15.4	12.7
34486	14.0	14.9	10.3
34487	13.4	14.1	9.4
34488	12.8	12.9	9.4
34489	10.6	10.3	6.8
34490	7.7	7.2	5.0
34491	6.2	5.9	4.0

and composed of only two longitudinal plates in this specimen. The crural bases are fused to the inner socket ridges and descend almost vertically to the floor of the valve, forming short thin tabellae. The spiral brachidium consists of at least three whorls per spire.

Occurrence and abundance.—This is a very rare species in the Lower Burlington Limestone of Pike County, Missouri. It seems to be restricted to the *Cryptoblastus* Zone or white chert beds. Rowley's dozen or so specimens, including types, are in the collections of the University of Illinois. Butts (1941) illustrated a specimen of this species from the Price Formation of Virginia. The author has collected several mostly poorly preserved specimens from the white chert beds at the Louisiana City Quarry, Pike County, Missouri.

Punctothyris kenwoodensis, new species
Figs. 2E, 5–7

Holotype.—CMNH 34485. Collected by the author from the St. Joe Limestone near Kenwood, Mayes County, Oklahoma.

Paratypes.—CMNH 34486–93, all from the same collection as the holotype.

Description.—Medium size for the family, strongly and subequally biconvex, with subovate outline; maximum width attained near midlength; lateral profile sublenticular to guttate; lateral extremities well rounded in all growth stages; anterior commissure uniplicate; fold and sulcus narrow, moderately developed, but usually well defined; ornament consisting of 8 to 11 rounded costae on the flanks and zero to three in the sulcus; bifurcations limited to lateral sulcal costae and occasionally sulcus or fold-bounding costae; intercostal furrows about the same width as the costae or slightly narrower; surface covered with tiny hollow papillae or spinules, crudely arranged in quincunx, and which terminate in secondary shell layer; shell substance impunctate.

Pedicle valve strongly and evenly inflated in large specimens, slightly thicker than

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Fig. 6.—*Punctothyris kenwoodensis,* new species; part of a growth series of seven specimens (also see Fig. 5); A–T, ventral, dorsal, lateral, posterior, and anterior views of four paratypes, CMNH 34487–9, 34491; all ×3.

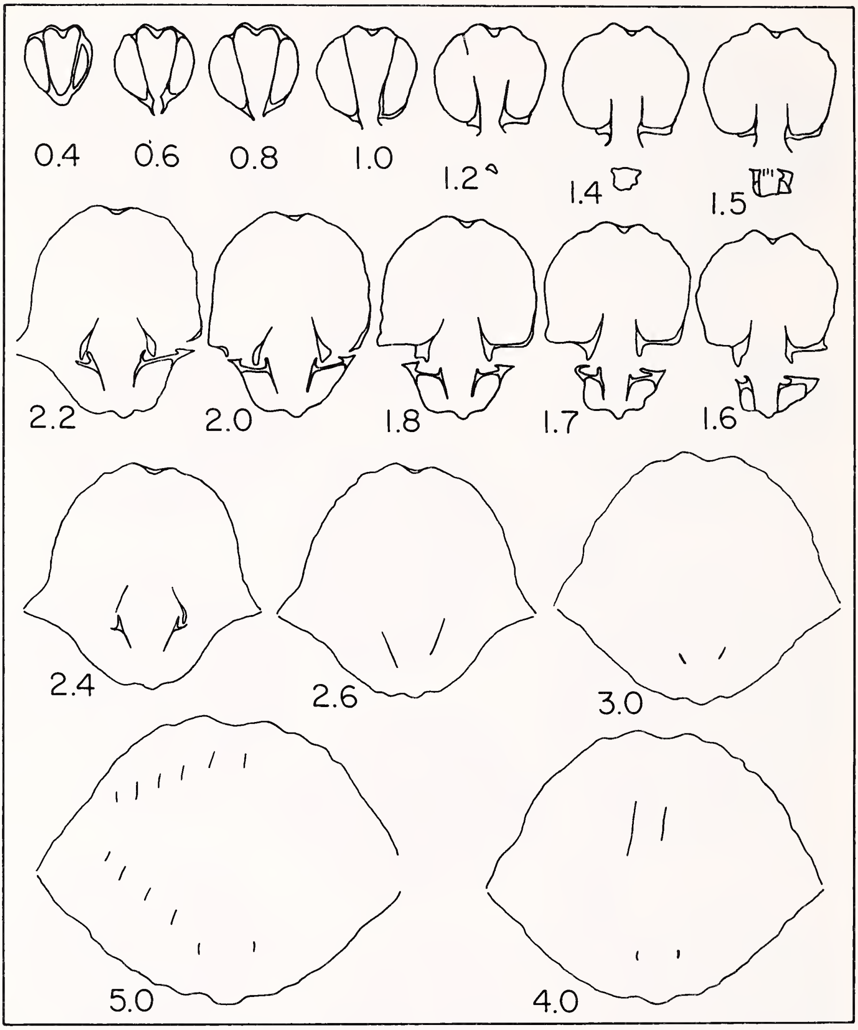

Fig. 7.—Transverse serial sections of *Punctothyris kenwoodensis,* new species, paratype CMNH 34493, ×4. Section numbers refer to distance in millimeters from the ventral beak.

opposite valve; maximum thickness attained slightly posterior to midlength; umbonal region moderately inflated; flanks slightly convex in profile, sloping steeply to lateral margins; cardinal extremities slightly compressed, well rounded; beak small, incurved; delthyrium about as wide as high with outwardly flaring stegidial plates; sulcus originating in beak region, becoming gradually wider, deeper, and rounded anteriorly; sulcus-bounding costae variably developed, sometimes distinctly coarser than those of flanks, at other times less well differentiated; costae near lateral extremities very weak, obscurely developed; sulcal costae rarely lacking as in Fig. 5A, but a median costa is normally developed.

Pedicle valve interior with very short thin dental adminicula and a low medial myophragm that originates in the beak region and extends forward well beyond the dental adminicula; impression of muscle field not discernible in transverse sections; teeth of moderate size.

Brachial valve inflated in larger specimens but never quite as convex as opposite valve; maximum thickness attained near or slightly posterior to midlength; umbonal region moderately inflated, projecting posterior to the hingeline; dorsal beak inconspicuous, incurved; dorsal interarea low, anacline; fold originating in umbonal region, rising gradually anteriorly to form moderately developed rounded fold; fold well delimited from flanks by fold-bounding furrows; ornament similar to that of opposite valve.

Brachial valve interior with very small striate cardinal process composed of three or four vertical plates; crural bases fused with inner socket ridges to form short thin nearly vertical tabellae; adductor impressions not discernible in transverse section; spiralia composed of at least six whorls.

Distinguishing characters.—This species is characterized by its ovate outline, medium size (Table 2), with 8 to 11 costae on the flanks, and zero to three costae in the sulcus.

Comparisons.—The differences between this species and *P. argus* Hyde and *P. schucherti* (Rowley) are discussed above under those species. *Punctothyris inusitata,* new species, differs from *P. kenwoodensis* in being smaller, having a more transverse outline, a narrower less inflated ventral umbonal region, and 13 lateral costae.

Occurrence and abundance.—This species is based on a single collection of 34 specimens from the steeply dipping flank beds of an abandoned quarry in a small bioherm in the St. Joe Limestone near Kenwood, SE ¼, SE ¼, Sec. 11, T.21 N., R.21 E., Mayes County, Oklahoma. The diverse brachiopod fauna from this bioherm points to a correlation with the Fern Glen Fm.—Dolbee Creek Limestone interval in the Mississippi Valley region.

Punctothyris inusitata, new species
Figs. 2G, 3A–G

Holotype.—CMNH 34495. Collected by the author from the Chouteau Limestone near Warren, Marion County, Missouri.

Paratypes.—CMNH 34494, 34496, from the same collection as the holotype.

Description.—Smaller than average for the family, with transversely subovate outline; maximum width attained at about midlength; lateral extremities rounded in all growth stages; anterior commissure uniplicate; sulcus narrow, moderately developed, well defined; ornament consisting of 13 simple rounded costae on the flanks and three or four costae in the sulcus, the median costa rarely bifurcating; lateral sulcal costae bifurcate from fold-bounding costae; rarely one lateral flank costa may bifurcate from sulcus-bounding costa; intercostal furrows narrower than costae; almost entire surface covered with densely spaced very fine hollow papillae or spinules, roughly arranged in quincunx; shell substance impunctate.

Table 3.—*Measurements in millimeters of the types of* Punctothyris inusitata.

CMNH number	Length	Width	Thickness
34494	±9.8	12.3	±4.6
34495	9.1	±10.7	±4.2
34496	6.7	7.9	±3.6

Pedicle valve moderately inflated with maximum thickness attained slightly posterior to midlength; umbonal region moderately inflated; beak small, narrow, incurved, projecting posterior to hingeline; flanks moderately convex, sloping evenly to lateral margins; cardinal extremities rounded, slightly compressed, interarea of moderate height, narrow, triangular, weakly concave, catacline to slightly apsacline, with weak faint vertical striae on the primary layer; delthyrium about as wide as high; stegidial plates thin, short; sulcus originating in beak region, becoming gradually deeper and rounded anteriorly; sulcus moderately well delimited from flanks; lateral costae becoming finer and indistinct laterally.

Pedicle valve interior with short thin dental adminicula; other details not observed.

Brachial valve unknown.

Distinguishing characters.—This species is characterized by its transversely ovate outline with 13 costae on the flanks and three or four in the sulcus, the median costa rarely bifurcating.

Comparisons.—The differences between this species and the other three species described in this paper are noted above. Table 3 gives measurements of this species.

Remarks.—Although the lack of dorsal interiors obviates an absolutely certain generic assignment, I have little doubt about placing this new species in the genus *Punctothyris.* Repeated collecting attempts to find brachial valves or additional specimens of any kind have failed. The macro- and micro-ornament leave no doubt that this is a new species and of special interest because of its occurrence in Kinderhookian strata.

Occurrence and abundance.—The above description is based on a single collection of only six pedicle valves, the three best of which are illustrated herein. These specimens were collected by the author from a roadcut in the Chouteau Limestone about one mile south of Warren, NW ¼, SE ¼, Sec. 2, T.57 N., R.8 W., Marion County, Missouri.

ACKNOWLEDGMENTS

I thank Profs. Stig Bergstrom and D. B. Blake for the loan of type materials in their care. Albert Kollar expertly prepared the serial sections of *Punctothyris kenwoodensis.* J. T. Dutro, Jr., and R. D. Hoare made useful suggestions for the improvement of this paper for which I am most grateful.

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UTILITY OF MORPHOLOGICAL DISTANCE MEASURES AND CLUSTERING ALGORITHMS: A TEST USING PHYLLOSTOMID BATS

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Abstract

Results of three measures of morphological distance (M-statistic, Mahalanobis' D^2, and Euclidean distance) are calibrated on the basis of three simple test criteria against nine taxa of phyllostomid bats whose morphological (phenetic) relationships are unequivocal. Eighteen different permutations of distance algorithm, data transformation, morphological measurement, and clustering algorithm were used to evaluate major criticisms that have been directed against morphological distance measures. The M-statistic is shown to be no less successful at meeting the test criteria than are the other two measures. However, the type of clustering algorithm used has a very definite effect on the representation of the measure of morphological distance on a one dimensional scale.

Introduction

Man's attempts to quantify his level of morphological distinctness from his nearest living relatives have been controversial. This contro-

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versy stems, in part, from disagreement about which morphological characteristics should be used, how they should be transformed, and what distance metrics should be calculated from them. Cherry et al. (1978) described a measure of morphological difference, the distance statistic M, to compare the morphological relationships of frogs, chimpanzees, and humans. The M-statistic has been cited as more valuable than other similar statistics for "broad comparative studies of evolution at the organismal level" (Kunkel et al., 1980:1061), but has also received criticism on several points (Findley, 1979; Atchley, 1980; Cherry et al., 1982). More recently, Cherry et al. (1982) compared the facility of the M-statistic with three other distance metrics in accurately portraying morphological relationships of a broad selection of tetrapod vertebrates. They found all four distance metrics to be highly correlated with distance in a taxonomic hierarchy based primarily on a phenetic classification. They used such a wide variety of taxa, including many groups for which relationships are poorly understood, that the accuracy of the distance metrics may not be well represented in their tests. This study describes tests to evaluate the M-statistic and two more conventional methods (Mahalanobis' D^2, Mahalanobis, 1936; and Euclidean Distance, Sneath and Sokal, 1973) by examining nine species of bats whose morphological features are so obvious that certain phenetic relationships should result from any valid measure of morphological distinctness. Additionally, we investigated the efficacy of type of measurement, transformation, and clustering algorithm in achieving a satisfactory classification. Two different sets of measurements were used. The first, labelled "bats" are those frequently used by bat taxonomists; the second, labelled "frogs" are ones considered applicable to all vertebrates, including those as specialized as frogs or apes (Cherry et al., 1978). A comparison of results from the two sets of measurements allows estimation of the extent to which choice of measurements affects results (Findley, 1979). Cherry et al. (1978) used a ratio transformation of their data to eliminate size as a factor *per se.* Our measurements were ratio and log transformed as well as untransformed in order to evaluate Atchley's (1980) criticism of the instability of ratio transformations. Combinations of measurements and transformations were then used in each of the distance statistics. Finally, taxonomists conveniently use cluster analysis as a primary technique for portraying morphological relatedness in one dimension, so we applied three clustering algorithms to each combination of measurements, transformations, and distance algorithms—Unweighted Pair Group Method using Arithmetic Averages (UPGMA, Sneath and Sokal, 1973); minimum distance (single linkage, Sokal and Sneath, 1963), and maximum distance (complete linkage, Johnson, 1967).

The basis for the calibration was to choose species whose morphological relationships were sufficiently obvious that the relative nature of the distance values and expected patterns of phenetic clustering would be predictable. Inaccuracies could be identified when calculations misrepresented the morphological relationships of these species.

In order to test the power of morphological distance metrics in accurately portraying the phenetic relationships of a group of organisms, those relationships must already be well understood. Furthermore, the probability of choosing a group of organisms that would provide a rigorous test would be increased if other aspects of their relatedness were also well known. Therefore, we chose nine species of New World leaf nosed bats of the family Phyllostomidae for which extensive karyological (Baker and Bass, 1979; Baker, 1979; Haiduk and Baker, 1982) molecular (Honeycutt et al., 1981; Baker et al., 1981), and morphological (Griffiths, 1982; Hood and Smith, 1982, 1983; Smith and Starrett, 1979) data are available.

The morphological relationships of the bat species chosen for this study can be grouped into two major categories reflective of their feeding habits. One group is the three species of vampire bats (recognized as three monotypic genera, *Desmodus, Diphylla,* and *Diaemus*). The other group is composed of five species of nectar and fruit eaters, which have elongated rostra (taxa examined were *Phyllonycteris aphylla, Erophylla sezekorni, Glossophaga soricina, Monophyllus redmani,* and *M. plethodon*). It is a critical assumption of this study that the three species of vampires more closely resemble each other than any nectar-feeding species and that the five nectar-feeders more closely resemble each other than any vampire. The first test is that any combination of measurements, transformations, distance computations, and clustering algorithms which does not distinguish the two major groupings will be judged an invalid measure of morphological distinctiveness.

The second test involves the ninth taxon examined in the study (*Brachyphylla cavernarum*). *Brachyphylla* is also a nectar and fruit eater but is so morphologically distinct that bat systematists have encountered considerable problems in determining its evolutionary origin (Baker and Bass, 1979; Griffiths, 1982, 1985). Only one point concerning *Brachyphylla* is critical, however. Because of its robust size, stocky build, and shortened snout, *Brachyphylla* is sufficiently morphologically distinct, from both the long-rostra nectar feeders and vampires, that it should not be classified within either group. Relative to the two groups, its position should be that of an outlier. Failure to place *Brachyphylla* as an outlier to the vampires and long-rostra nectar feeders would result in rejection of that method as a valid one.

The third test is within the long-rostra group. We chose two sibling species (*Monophyllus redmani* and *M. plethodon*) which are morphologically so similar that it is necessary to have detailed cranial measurements for species identification (Schwartz and Jones, 1967). The final criterion for a valid measure of morphological distinctiveness is that the method places each of the two species of *Monophyllus* closer to each other than to any of the other taxa examined.

METHODS AND MATERIALS

In all but one case (*Diaemus youngi*, n = 9) 10 adult individuals of each species were measured from the collections of The Museum of Texas Tech University and The Texas Cooperative Wildlife Collection at Texas A&M University. Specimens examined are listed in Appendix I.

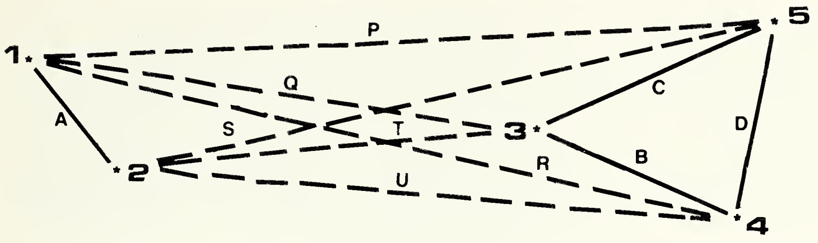
Two sets of measurements were chosen. For their study, Cherry et al. (1978) chose a set of nine morphological measurements previously used to assess shape changes in frogs (Jameson et al., 1966; Jameson and Richmond, 1971) to avoid bias toward humans and against frogs. We used these nine measurements, taken from all major parts of the body, in the attempt to evaluate Cherry et al.'s statement that "almost any evolutionary change in body shape would be reflected in at least one of these measurements" (Cherry et al., 1978:210). Whereas, the morphological uniqueness of bats in comparison with either higher primates or frogs made it somewhat difficult to modify these measurements they are: 1) tibia length; 2) forearm length; 3) hindfoot length; 4) greatest length of skull; 5) width of maxilla at first incisors; 6) vertebral length; 7) distance from anterior margin of auditory meatus to lacrimal canal; 8) distance from lacrimal canal to anterior margin of nasals; and 9) mastoidal breadth.

We also chose nine highly repeatable measurements from bats, some of which obviously reflect much of the evolutionary change within the order and others which are general mammalian measurements. These are: 1) total length; 2) tail length; 3) hindfoot length; 4) ear length; 5) forearm length; 6) length of metacarpal of digit five; 7) length of extended calcar and leg; 8) greatest length of skull; and 9) mastoidal breadth. All measurements except total, tail, hind foot, and ear lengths were measured on museum study skins and skulls to the nearest 0.1 millimeter with dial calipers. The four remaining measurements were taken directly from museum specimen labels. All measurements are given in Appendix II. A comparison of the results from the nine measurements of Cherry et al. (1978) with the results from the nine measurements selected especially for bats allows the opportunity to estimate the extent to which choice of measurements affects results (Findley's, 1979, criticism).

Both sets of measurements were ratio and log transformed and utilized in each of the three distance statistics. Comparison of the three types of distance matrices (Appendix III) allows the opportunity to evaluate the role correlation of characters plays in distance measures (Atchley's, 1980, criticism).

In this study, M-statistics were calculated using a FORTRAN program and Mahalanobis' D^2 and Euclidean distances were generated from SAS programs (Barr et al., 1979). Clustering analyses were performed on each of the distance matrices using the Unweighted Pair Group Method using Arithmetic Averages (UPGMA) with TAXON from the Numerical Taxonomy System (NT-SYS) package (Rohlf et al., 1974; Sneath and Sokal, 1973), and minimum distance (Johnson, 1967) and maximum distance method (Johnson, 1967) using the FACTOR, SCORE, and CLUSTER procedures of SAS (Sneath and Sokal, 1973; Barr et al., 1979). Fig. 1 demonstrates how candidates are merged with existing clusters in each of the three clustering methods.

The average distance method is the most widely used on taxonomic data. It selects clusters so that the average distance between members in the same cluster is less than the average distance between members of different clusters. A candidate will join a cluster if the average distance between it and the center of the cluster is less than the average distance to the center of any other cluster. The corresponding criterion for the maximum



TAXA 1 & 2 WILL BE PLACED IN A SEPARATE CLUSTER FROM TAXA 3,4 & 5 IF:

AVERAGE DISTANCE $\frac{A+B+C+D}{4} < \frac{P+Q+R+S+T+U}{6}$

MAXIMUM DISTANCE MAX (B,C,D) < MIN (P,Q,R,S,T,U)
A < MIN (P,Q,R,S,T,U)

MINIMUM DISTANCE A < MIN (P,Q,R,S,T,U)
MIN (B,D) < MIN (Q,T)
MIN (B,C) < MIN (P,S)
MIN (C,D) < MIN (R,U)

Fig. 1.—Criteria by which Average Distance, Minimum Distance, and Maximum Distance clustering algorithms form clusters; further details in text.

Taxa	Distance value between taxa
1,2	A
3,4	B
3,5	C
4,5	D
1,3	P
1,4	Q
1,5	R
2,3	S
2,4	T
2,5	U

distance method is that no species within a cluster can be further away from any species in the cluster than from a species outside its cluster. In the minimum distance method a species will be placed according to the cluster membership of the species closest to it. Essentially, maximum and minimum clustering methods merge two clusters on the basis of a single value; the greatest distance or least distance value, respectively, between

Table 1.—*Results of test of resolution of different combinations of measurements, distance statistics and transformation of data from nine taxa of bats. OK = taxa correctly classified; F = taxa incorrectly classified. Test 1 was correct separation of vampires and long-rostra nectar feeders into distinct groups. Test 2 was distinguishing* Brachyphylla *as an outlier from both vampires and long-rostra bats and Test 3 was the association of two sibling species nearer to each other than to any other taxon. M = M-statistic; D^2 = Mahalanobis distance; Eu = Euclidean distance; U = untransformed data; Ratio = ratio transformed data; Log = log transformed data; Bat = measurements selected to encompass bat variation; Frog = measurements selected by Cherry et al. (1978) for general changes in body shape.*

Distance, transformation, kind of measurement	Clustering method								
	Maximum test			Average test			Minimum test		
	1	2	3	1	2	3	1	2	3
M—U—Bat	F	OK	F	F	OK	F	OK	OK	F
M—U—Frog	F	F	F	F	OK	F	OK	OK	F
M—Ratio—Bat	OK	F	OK	F	F	F	OK	F	OK
M—Ratio—Frog	F	F	F	F	F	F	OK	OK	F
M—Log—Bat	F	F	OK	F	F	F	OK	OK	OK
M—Log—Frog	F	F	F	F	F	F	OK	OK	F
D^2—U—Bat	F	F	F	F	F	F	OK	OK	F
D^2—U—Frog	F	OK	F	OK	OK	F	OK	OK	F
D^2—Ratio—Bat	F	F	OK	OK	OK	OK	OK	OK	OK
D^2—Ratio—Frog	F	F	F	OK	OK	F	OK	OK	F
D^2—Log—Bat	F	F	F	OK	OK	F	OK	OK	F
D^2—Log—Frog	F	F	F	OK	OK	F	OK	OK	F
Eu—U—Bat	OK	OK	F	OK	OK	F	OK	OK	F
Eu—U—Frog	F	OK	F	OK	OK	F	F	OK	F
Eu—Ratio—Bat	OK	OK	F	OK	OK	F	OK	OK	F
Eu—Ratio—Frog	F	F	F	F	F	F	OK	OK	F
Eu—Log—Bat	OK	OK	F	OK	OK	F	OK	OK	F
Eu—Log—Frog	F	OK	F	F	F	F	OK	OK	F

points, whereas UPGMA forms clusters on the basis of an average value. In data such as those displayed in Fig. 1, the different methods would return the same result. However, in some circumstances the results can be very different. If the five species were arranged in a line, it is possible that species 3 might be nearest to species 4, and species 4 be nearest species 5. Yet the distance between species 2 and 3 might be smaller than that between species 3 and 5. Here minimum and maximum distance methods would give different results.

RESULTS

Results of the different combinations of methods are shown in Table 1. Only thrice were all three test criteria met (Mahalanobis' D^2 ratio transformed bat measurements with average distance clustering and minimum distance clustering, and M-statistic log transformed bat measurements). Maximum distance clustering showed a low level of success in meeting the three test criteria with minimum distance clustering (14 successes out of 54 tries); average distance clustering was somewhat more successful, especially with Mahalanobis' D^2 distances (21 out of 54), and minimum distance clustering consistently succeeded in meeting the first two test criteria for all combinations of measurements, data transformations, and distance statistics (failing only twice), but was ineffective (three successes out of 18 tries) on the third criterion.

Chi-square tests of the data show minimum distance clustering (17 successes) to be significantly more successful in meeting the first test criterion than the maximum distance (4 successes) or UPGMA clustering (nine successes)($\chi^2_1 = 9.45$, $P < 0.01$). The minimum distance clustering was also marginally better than the other clustering methods on the second test criterion ($\chi^2_1 = 3.66$, $P < 0.06$) with 17 successes versus seven successes for maximum and 11 successes for UPGMA clustering. However, none of the three clustering algorithms was consistently more successful in properly grouping the two *Monophyllus* species, three versus one versus three successes for maximum, average and minimum clustering, respectively.

Findley's (1979) point regarding choice of characters to be measured is well taken. But for these data at least, the measurements chosen specifically to emphasize variation within bats were not significantly more effective in differentiating between the nine species than were the measurements used originally for frogs! (43 successes for "bats" versus 29 for "frogs" ($\chi^2_1 = 1.66$, $P > 0.05$). Atchley's (1980) criticism of the use of a ratio transformation by Cherry et al. (1978) is not applicable to our data because ratio transformed, log transformed, and untransformed data were almost equally successful in meeting the three test criteria (25, 23, and 24 successes, respectively). The three distance statistics also showed no consistent differences in meeting the three test criteria ($\chi^2_1 = 2.1$, $P > 0.05$). This suggests that Atchley's (1980) criticism of the M-statistic for its disregard of correlation between characters is, similarly, not applicable to these data. Kunkel et al. (1980) defended the use of the M-statistic stating that its weakness concerning correlation between characters is compensated for by its superiority with small sample sizes, although Cherry et al. (1982) found small sample sizes used with both the M-statistic and Mahalanobis' D^2 led to overestimates of D values. We used a small sample size ($n = 10$) yet the M-statistic was no more successful at meeting the three criteria than were Mahalanobis' D^2 and Euclidean distances.

Distance values, the input for the clustering algorithms, between each possible pair of the nine species were arranged so that the nearest distance (smallest value) and farthest distance (largest value) from any one species to the other eight could be examined for each of the combinations of methods. All the permutations consistently placed the same groups of species in nearest or farthest proximity to one another. Examination of these actual distances between taxa pairs demonstrates their relative insensitivity to the kinds of measurements, transformations, or distance algorithms used. This suggests that the most critical step, by far, in producing a successful clustering involves the final step—the choice of the clustering algorithms itself.

DISCUSSION

Distance Statistics

Following Findley's (1979) observation that by the particular selection of appropriate anatomical features one could show great similarity or dissimilarity on the basis of distance values, the nine bat measurements in this study included morphological traits that emphasized variation in the bat taxa examined. The nine measurements of Cherry et al. (1978) were said to be chosen objectively to show evolutionary change in all major parts of the body of vertebrate animals. Comparison of results based on the two sets of measurements showed neither set to be superior in successfully meeting our three criteria for differentiating between the nine taxa.

The merits of ratio transformation of data have been hotly debated (Atchley et al., 1976; Atchley, 1978; Hill, 1978). Whereas ratio transformed data resulted in some of the more aberrant placements of taxa, only two of the three sets of measurements, transformations, distance statistics, and clustering algorithms that met all three test criteria involved ratio transformations. Atchley's (1980) criticism of the use of a ratio transformation by Cherry et al. (1978) is not supported by this study because neither ratio transformed, log transformed nor untransformed data were consistently successful in meeting the three test criteria. The three distance statistics showed no consistent differences in meeting the three test criteria suggesting that both Atchley's (1980) criticism of the M-statistic for disregard of correlation between characters and that of Kunkel et al. (1980) concerning Mahalanobis' D^2 over-compensation for correlation between characters are not totally warranted.

Clustering Algorithms

Rohlf (1962) and Sokal and Rohlf (1962) found average distance clustering with UPGMA to be superior to other clustering algorithms and Sneath and Sokal (1973) cite UPGMA as the most frequently used algorithm. Minimum distance clustering, however, has been viewed as defective because of a tendency to cluster together taxa linked by chains of intermediates (Everitt, 1974), and maximum distance clustering has been accused of "space dialating" extremes (Sneath and Sokal, 1973). Yet, none of the three clustering algorithms was consistently able to meet all three test criteria. Whereas the distance statistics yielded the same results, the clustering algorithms showed different levels of success in accurately portraying these matrices.

Minimum distance clustering, even with its alleged defect of "chaining," was the only clustering algorithm consistently successful in meeting the test criteria. One difficulty encountered in cluster analysis is that each algorithm carries with it assumptions about the type of structures present in the data; for example, the average distance method assumes that taxa will be arrayed spherically in hyperspace (Sokal and Michener, 1967; Everitt, 1974). This study suggests that such spherical clusters may not be the case with these animals and that by allowing for chains of taxa rather than discrete spheres of taxa, minimum distance clustering gives a more accurate representation of phenetic relationships within this group than does average distance or maximum distance clustering.

CONCLUSIONS

Results of this study suggest that the three principal criticisms directed against the M-statistic are only of minor importance. Regardless of choice of measurements and allowance for correlation between characters or type of data transformation, the M-statistic, Mahalanobis' D^2, and Euclidean distance statistics yield the same results. The M-statistic is shown to be no worse, but certainly no better at accurately measuring morphological distance than either of the other two distance algorithms.

It is of major importance, however, that none of the clustering algorithms could accurately portray the phenetic relationships of the nine taxa on the basis of all three test criteria. This study describes inconsistencies in how the three clustering algorithms interpret the distance matrices. Choice of the best clustering algorithm for a group of taxa hinges on preconception of how those taxa are arrayed in hyperspace. Perhaps, as taxa follow different evolutionary tracks resulting in different patterns in hyperspace, one type of clustering algorithm will most accurately mirror phenetic relationships of one group, whereas a different clustering algorithm will be required to accurately portray phenetic relationships of another group.

Reasons underlying different results from the three clustering algorithms are not evident here. The basis for discordant results may be some facet of the clustering algorithms or it may be traced to some earlier step in the process of measurement, transformation, and distance metric calculation. For example, in our data set, the absence of a tail measurement in desmodontines may confound clustering of the other six taxa which have short and relatively longer tails. Taxa with short tails may actually cluster closer to taxa with no tails than with those having long tails. Additionally, the consistent failure of test 3, grouping the sibling species of *Monophyllus* is striking. Perhaps the distance statistics used do not accurately portray the extreme morphological similarity of these bats. In such a case, no combination of transformation and clustering could be expected to give predictable results. Alternatively, both the "frog" and "bat" measurements may have been too generalized to be sensitive to variation at this level, or none of the techniques adequately dealt with size bias. Inherent weaknesses of the often indiscriminantly used tool of cluster analysis are made apparent, however. There is now a call for more rigorous tests using other well-characterized taxa to enhance understanding of the circumstances of applicability of distance metrics and clustering algorithms to evolutionary studies.

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APPENDIX I

Specimens Examined

Brachyphylla cavernarum.—GUADELOUPE; Basse-Terre, 1 km S, 4 km W Vernou, TTU 20968, 1 km W Vernou, TTU 20967, 2 km N Baillif, TTU 20965, Grand-Terre, 1 km N, 1 km W St. Francois, TTU 20974.

Diphylla ecaudata.—HONDURAS; Morazan, 0.3 mi SE Sabana Grande, TTU 30669, Olancho, 40 km NE Catacamas, TCWC 19685, TCWC 19686. MEXICO; Tamaulipas, 67 km S Cd. Victoria on Mex. 85, TTU 10171, Vera Cruz, Ojo de Agua del Rio Atoyac, TTU 10000–10001, 10157, Yucatan, Cueva de Spuril, 3 km NW Komchen, TTU 25899, 3 km S, 1 km W Calcehtoc, TTU 25900. UNITED STATES; Texas, Val Verde Co., Comstock R. R. Tunnel, TTU 5658.

Desmodus rotundus—MEXICO; Tamaulipas, 68 km S Cd. Victoria, Mex. 85, TTU 8228, Rio Corona, Mex. 101, N Cd. Victoria, TTU 8578, Rancho del Cielo, TTU 7356–7357, TTU 7359–7360, Veracruz, 76 km NW Taxpan, TTU 8193–8195, TTU 8190.

Diaemus youngi.—COSTA RICA; Guanacaste, Finca la Pacifica, 4 km NW Canas, TCWC 22533. EL SALVADOR; La Paz, 3 mi NW La Herradura, TTU 27591. NICARAGUA; Managua, 3 km N Masachapa, TTU 30667, Zelaya, 3 km NW Rama, TTU 30668. TRINIDAD; Maracas Valley, TTU 5428, TTU 5232–5233, Los Cueveus, TTU 5411, St. Patrick, La Brea, TTU 26888.

Erophylla sezekorni.—PUERTO RICO; El Verde Research Station, El Yunque Natl. Forest, TTU 8922, TTU 8923, TTU 8919, El Toro, El Yunque Natl. Forest, TTU 8906–8907, 1 mi W Corozal, TTU 8937–8941.

Glossophaga soricina.—MEXICO; Hidalgo, El Suspiro, 1 km N, 4 km W Tahuetlan, TTU 24192, 4 mi S San Felipe Orizatlan, TTU 15458, TTU 15464, 8 mi S Tlanchinol, TTU 24194, San Luis Potosi, Cueva de Los Savinos, 8 mi NE Cd. Valles, TTU 8341–8342, Yucatan, Colegio Peninsular Colonia Bueno Vista, Merida, TTU 25892–25893, Cueva de Spuril, 3 km S, 1 km W Calchetoc, TTU 25890–25891.

Monophyllus plethodon.—DOMINICA; St. Joseph Parish, Clark Hall, TTU 9337, TTU 31330–31331, St. Paul Parish, Springfield, TTU 31329, 1 mi from mouth of Layou River, TTU 31332. GUADELOUPE; Basse-Terre, Bains Jaunes, 2.5 km E Saint Claude, TTU 20795–20796, 1 km W Vernou, TTU 20798–20800.

Monophyllus redmani.—PUERTO RICO; El Toro, El Yunque Natl. Forest, TTU 9791, El Verde Research Station, El Yunque Natl. Forest, TTU 8927–8928, 1 mi W Corozal, TTU 8934–8936, TTU 9815–9817.

Phyllonycteris aphylla.—JAMAICA; St. Ann Parish, Orange Valley, TTU 21901–21908, TTU 21923–21925.

APPENDIX II

Measurements (mm) from Specimens Examined

Number	TTL	TL	EL	HF	FA	GLS	CL	MD5	MB
	TB	GLS	NL	FA	VL	MB	ET	HF	EN
Brachyphylla cavernarum									
TTU 8896	86.0	0.0	20.0	19.0	66.5	31.6	6.3	58.0	14.8
	26.6	31.6	0.9	66.5	54.4	14.8	12.6	19.0	7.5
TTU 9819	99.0	6.0	22.0	17.0	65.6	31.5	4.7	57.6	14.8
	26.1	31.5	0.8	65.3	67.5	14.8	11.8	17.0	8.1
TTU 9820	98.0	7.0	21.0	15.0	66.6	31.5	4.5	57.3	14.9
	25.6	31.5	1.0	66.6	66.5	14.9	12.5	15.0	8.1
TTU 8892	83.0	6.0	22.0	20.0	62.5	32.3	4.8	51.9	15.2
	21.2	32.3	0.8	62.5	50.7	15.2	12.6	20.0	8.0
TTU 20968	97.0	5.0	22.0	21.0	65.6	31.8	6.8	55.9	15.0
	25.6	31.8	0.7	65.6	65.2	15.0	12.3	21.0	8.2
TTU 20967	102.0	9.0	23.0	20.0	62.3	30.7	5.8	56.3	14.9
	25.0	30.7	0.7	62.3	71.3	14.9	12.5	20.0	7.8
TTU 20965	101.0	6.0	22.0	20.0	64.7	31.5	7.8	55.2	14.6
	24.5	31.5	0.7	64.7	69.5	14.6	13.0	20.0	8.0
TTU 20974	98.0	8.0	24.0	22.0	64.0	30.3	4.1	54.9	14.3
	24.5	30.3	0.6	64.0	67.7	14.3	12.3	22.0	7.6
TTU 8893	86.0	0.0	18.0	16.0	64.5	30.1	4.1	54.5	14.5
	23.3	30.1	0.7	64.5	55.9	14.5	11.9	16.0	7.9
TTU 8894	91.0	0.0	18.0	17.0	61.3	30.7	5.9	54.8	14.7
	22.5	30.7	0.7	61.3	60.3	14.7	12.0	17.0	7.4
Diphylla ecaudata									
TTU 10171	75.0	0.0	7.0	18.0	54.2	22.9	5.0	52.2	11.5
	22.3	22.9	1.2	54.2	52.1	11.5	6.7	18.0	6.5
TTU 10000	88.0	0.0	13.0	14.0	53.6	22.5	8.0	50.8	11.8
	21.2	22.5	1.2	53.6	65.5	11.8	7.0	14.0	6.1
TTU 10001	70.0	0.0	13.0	15.0	54.5	22.6	7.7	50.6	11.8
	21.0	22.6	1.0	54.5	47.4	11.8	6.8	15.0	5.6
TTU 10157	76.0	0.0	12.0	18.0	55.1	23.2	7.5	53.7	11.9
	22.1	23.2	1.2	55.1	52.8	11.9	7.0	18.0	5.9
TTU 25899	78.0	0.0	14.0	18.0	48.9	21.8	6.5	49.2	11.2
	19.9	21.8	1.0	48.9	56.2	11.2	6.5	18.0	5.8
TTU 25900	80.0	0.0	15.0	17.0	50.6	22.0	6.0	50.8	11.4
	20.5	22.0	1.1	50.6	58.0	11.4	7.1	17.0	5.8
TTU 5658	83.0	0.0	16.0	18.0	51.8	23.0	6.2	51.8	12.2
	19.6	23.0	1.2	51.8	60.0	12.2	7.1	18.0	5.6
TTU 30669	84.0	0.0	9.0	17.0	53.8	23.0	7.6	52.8	12.6
	20.6	23.0	1.2	53.8	61.0	12.6	9.5	17.0	5.7
TCWC 19685	83.0	0.0	16.0	14.0	51.5	22.7	6.3	50.5	11.8
	18.7	22.7	1.3	51.5	60.3	11.8	9.2	14.0	5.2
TCWC 19686	87.0	0.0	16.0	16.0	55.3	23.5	5.5	55.0	12.2
	19.5	23.5	1.4	55.3	63.5	12.2	9.0	16.0	6.0

APPENDIX II—*Continued.*

	TTL	TL	EL	HF	FA	GLS	CL	MD5	MB
Number	TB	GLS	NL	FA	VL	MB	ET	HF	EN
				Desmodus rotundus					
TTU 8228	84.0	0.0	17.0	19.0	60.3	24.1	3.9	50.3	12.3
	24.0	24.1	0.6	60.3	59.9	12.3	8.1	19.0	5.8
TTU 8578	84.0	0.0	18.5	17.0	62.9	24.4	3.0	55.8	12.6
	25.9	24.4	1.1	62.9	59.6	12.6	7.8	17.0	6.0
TTU 7356	78.0	0.0	16.0	19.0	56.9	23.5	3.2	48.9	12.0
	23.8	23.5	0.8	56.9	54.5	12.0	7.0	19.0	5.9
TTU 7357	73.0	0.0	15.0	19.0	55.0	23.6	3.0	48.7	12.0
	22.7	23.6	0.7	55.0	49.4	12.0	7.2	19.0	5.9
TTU 7359	70.0	0.0	16.0	19.0	55.8	22.5	2.7	48.6	12.1
	22.4	22.5	0.4	55.8	47.5	12.1	7.0	19.0	5.9
TTU 7360	83.0	0.0	17.0	21.0	62.3	24.5	3.1	52.3	13.0
	25.2	24.5	0.7	62.3	58.5	13.0	7.9	21.0	5.8
TTU 8193	91.0	0.0	18.0	19.0	61.1	24.4	2.9	53.6	12.7
	24.6	24.4	0.8	61.1	66.6	12.7	7.8	19.0	6.0
TTU 8194	84.0	0.0	18.0	16.0	53.8	23.5	2.8	47.5	12.6
	22.8	23.5	1.0	53.8	60.5	12.6	7.7	16.0	5.9
TTU 8195	84.0	0.0	15.0	19.0	54.5	23.0	2.8	40.0	12.2
	24.2	23.0	1.0	54.5	61.0	12.2	7.3	19.0	5.9
TTU 8190	79.0	0.0	15.0	19.0	57.5	23.8	3.5	49.0	12.4
	24.2	23.8	0.7	57.5	55.2	12.4	7.3	19.0	6.2
				Diaemus youngi					
TTU 27591	95.0	0.0	14.0	21.0	53.7	25.0	5.8	49.0	13.4
	10.5	25.0	0.9	53.7	70.0	13.4	8.1	21.0	6.1
TTU 5411	79.0	0.0	16.0	14.0	47.3	23.6	3.2	43.6	12.2
	21.4	23.6	0.7	47.3	55.4	12.2	7.3	14.0	5.3
TTU 5428	77.0	0.0	17.0	17.0	48.6	23.7	4.0	45.8	12.4
	21.9	23.7	0.9	48.6	53.3	12.4	7.3	17.0	5.9
TTU 5233	54.0	0.0	14.0	17.0	48.1	23.9	3.8	43.8	11.6
	20.4	23.9	1.0	48.1	30.1	11.6	7.6	17.0	5.9
TTU 5232	53.0	0.0	15.0	17.0	48.4	23.1	3.7	46.0	12.4
	20.7	23.1	1.0	48.4	29.9	12.4	7.0	17.0	5.5
TTU 26888	87.0	0.0	11.0	18.0	50.3	23.7	5.2	46.9	12.4
	19.7	23.7	1.2	50.3	63.3	12.4	9.6	18.0	5.5
TTU 30667	87.0	0.0	15.0	20.0	55.3	25.4	6.1	49.6	13.6
	22.2	25.4	1.2	55.3	61.6	13.6	10.7	20.0	6.1
TTU 30668	90.0	0.0	12.0	19.0	56.9	26.0	5.3	53.0	13.3
	23.8	26.0	1.3	56.9	64.0	13.3	11.0	19.0	6.3
TCWC 22533	92.0	0.0	19.0	20.0	55.2	25.6	4.7	49.8	13.0
	23.6	25.6	1.2	55.2	66.4	13.0	10.2	20.0	6.4
				Erophylla sezekorni					
TTU 8922	80.0	14.0	18.0	14.0	47.1	24.0	3.2	38.4	10.5
	19.5	24.0	0.4	47.1	56.0	10.5	8.9	14.0	6.8

Appendix II—*Continued.*

Number	TTL TB	TL GLS	EL NL	HF FA	FA VL	GLS MB	CL ET	MD5 HF	MB EN
TTU 8923	74.0	15.0	17.0	14.0	44.0	23.6	3.1	39.3	10.5
	20.7	23.6	0.4	44.0	50.4	10.5	8.5	14.0	6.6
TTU 8919	79.0	13.0	19.0	13.0	45.9	24.2	2.8	37.1	10.7
	19.2	24.2	0.4	45.9	54.8	10.7	8.7	13.0	6.3
TTU 8937	79.0	11.0	15.0	14.0	47.9	24.2	2.8	38.8	11.0
	19.5	24.2	0.5	47.9	54.8	11.0	8.9	14.0	6.3
TTU 8906	82.0	13.0	15.0	14.0	47.1	24.8	3.2	39.4	10.6
	19.8	24.8	0.5	47.1	57.2	10.6	9.0	14.0	6.9
TTU 8941	74.0	12.0	17.0	14.0	46.6	24.3	2.9	38.3	10.6
	19.5	24.3	0.4	46.6	49.7	10.6	8.7	14.0	6.6
TTU 8940	73.0	12.0	19.0	14.0	47.0	23.8	3.3	38.6	10.6
	20.2	23.8	0.4	47.0	49.2	10.6	8.5	14.0	6.7
TTU 8939	79.0	14.0	19.0	14.0	49.1	23.9	3.0	40.0	10.8
	20.6	23.9	0.5	49.1	55.1	10.8	8.8	14.0	6.5
TTU 8938	75.0	13.0	15.0	14.0	47.2	24.8	2.9	38.4	11.0
	19.9	24.8	0.5	47.2	50.2	11.0	8.9	14.0	6.4
TTU 8907	75.0	15.0	15.0	15.0	47.2	24.4	3.4	39.0	10.7
	19.4	24.4	0.5	47.2	50.6	10.7	8.9	15.0	6.8
Glossophaga soricina									
TTU 25893	63.0	8.0	14.0	11.0	34.2	20.8	5.8	29.1	9.0
	12.8	20.8	0.3	34.2	42.2	9.0	7.2	11.0	5.4
TTU 25892	63.0	6.0	15.0	10.0	34.0	20.9	5.5	31.3	8.9
	–	20.9	0.4	34.0	42.1	8.9	7.5	10.0	5.5
TTU 25891	69.0	9.0	15.0	11.0	36.1	21.4	5.1	31.7	8.9
	14.2	21.4	0.4	36.1	47.6	8.9	7.5	11.0	5.7
TTU 25890	59.0	7.0	15.0	10.0	32.9	20.7	6.2	28.7	8.7
	12.5	20.7	0.4	32.9	38.3	8.7	7.0	10.0	5.4
TTU 8342	68.0	6.0	14.0	10.0	35.0	21.6	6.8	30.6	8.9
	13.8	21.6	0.4	35.0	46.4	8.9	7.7	10.0	5.5
TTU 8341	65.0	7.0	13.0	10.0	35.8	21.7	6.5	32.0	9.2
	13.0	21.7	0.4	35.8	43.3	9.2	7.5	10.0	5.9
TTU 24194	58.5	9.0	14.5	11.0	34.8	20.8	5.1	30.8	8.8
	12.5	20.8	0.2	34.8	37.7	8.8	7.6	11.0	5.2
TTU 15458	55.0	–	13.0	11.0	35.4	20.8	6.9	31.6	8.9
	12.8	20.8	0.3	35.4	34.2	8.9	7.0	11.0	5.3
TTU 15464	61.0	4.0	15.0	9.0	36.5	20.9	6.8	31.4	8.6
	12.7	20.9	0.3	36.5	40.1	8.6	7.3	9.0	5.6
TTU 24192	56.0	6.0	14.0	12.0	33.9	20.5	6.5	30.3	8.8
	12.0	20.5	0.2	33.9	35.5	8.8	7.1	12.0	5.4
Monophyllus plethodon									
TTU 9337	78.0	13.0	15.5	15.0	40.3	22.9	4.6	32.7	10.0
	17.0	22.9	0.5	40.3	55.1	10.0	8.2	15.0	6.1

APPENDIX II—*Continued.*

Number	TTL	TL	EL	HF	FA	GLS	CL	MD5	MB
	TB	GLS	NL	FA	VL	MB	ET	HF	EN
TTU 20795	79.0	13.0	15.0	17.0	39.1	23.3	4.1	29.6	10.0
	16.1	23.3	0.5	39.1	55.7	10.0	9.0	17.0	5.5
TTU 20796	81.0	13.0	16.0	13.0	42.0	23.6	3.6	32.8	10.1
	16.4	23.6	0.5	42.0	57.4	10.1	8.5	13.0	6.1
TTU 20798	79.0	12.0	15.0	9.0	40.8	23.3	3.7	32.3	9.5
	16.8	23.3	0.3	40.8	55.7	9.5	8.5	9.0	6.2
TTU 20799	80.0	13.0	13.0	13.0	41.0	23.4	4.0	31.9	9.6
	16.5	23.4	0.4	41.0	56.6	9.6	8.2	13.0	6.5
TTU 20800	74.0	11.0	16.0	13.0	40.9	23.2	3.7	31.3	10.1
	16.8	23.2	0.3	40.9	50.8	10.1	8.3	13.0	6.1
TTU 31329	78.0	14.0	16.0	12.0	41.1	23.0	3.1	33.1	9.6
	17.7	23.0	0.3	41.1	55.0	9.6	8.1	12.0	6.2
TTU 31330	78.0	12.0	15.0	14.0	40.9	23.6	3.5	30.4	9.5
	17.3	23.6	0.5	40.9	54.4	9.5	8.5	14.0	6.4
TTU 31331	78.0	12.0	14.0	14.0	40.0	23.6	2.8	30.5	9.6
	16.2	23.6	0.3	40.0	54.4	9.6	8.3	14.0	6.4
TTU 31332	72.0	12.0	15.0	13.0	40.1	22.9	3.5	31.6	9.6
	16.1	22.9	0.4	40.1	49.1	9.6	8.6	13.0	5.7
				Monophyllus redmani					
TTU 8933	61.0	7.0	9.0	14.0	36.8	20.0	4.2	28.5	8.5
	15.1	20.0	0.3	36.8	41.0	8.5	6.7	14.0	5.3
TTU 8927	48.0	6.0	10.0	11.0	35.7	19.8	4.0	28.5	8.2
	14.7	19.8	0.2	35.7	28.2	8.2	6.8	11.0	5.0
TTU 8928	52.0	6.0	8.0	11.0	35.6	19.9	3.4	28.1	8.1
	15.1	19.9	0.3	35.6	32.1	8.1	6.6	11.0	5.2
TTU 8935	61.0	10.0	11.0	12.0	36.0	19.8	3.6	28.5	8.2
	14.3	19.8	0.4	36.0	41.2	8.2	6.5	12.0	5.7
TTU 8936	51.0	—	10.0	10.0	35.3	19.3	4.1	26.6	8.1
	13.1	19.3	0.2	35.3	31.7	8.1	6.3	10.0	5.1
TTU 9791	65.0	10.0	9.5	11.0	36.1	19.7	4.3	28.5	8.2
	14.5	19.7	0.2	36.1	45.3	8.2	6.6	11.0	4.8
TTU 8934	53.0	6.0	13.0	11.0	36.4	19.8	3.8	27.8	8.2
	15.0	19.8	0.3	36.4	33.2	8.2	6.4	11.0	5.1
TTU 9816	62.0	8.5	9.5	12.5	36.3	20.1	4.0	28.6	8.5
	14.8	20.1	0.2	36.3	41.9	8.5	6.6	12.5	5.1
TTU 9815	60.0	10.0	10.0	12.0	35.7	19.5	4.7	28.6	8.2
	15.0	19.5	0.2	35.7	40.5	8.2	6.1	12.0	5.1
TTU 9817	63.0	10.0	9.0	12.0	36.3	19.3	4.0	28.6	8.3
	15.4	19.3	0.2	36.3	43.7	8.3	6.6	12.0	5.0
				Phyllonycteris aphylla					
TTU 21923	75.0	7.0	17.0	15.0	45.5	25.2	2.2	38.2	11.1
	22.9	25.2	0.9	45.5	49.8	11.1	8.6	15.0	7.9
TTU 21908	85.0	8.0	18.0	16.0	44.8	24.9	1.5	38.0	11.1

APPENDIX II—*Continued.*

	TTL	TL	EL	HF	FA	GLS	CL	MD5	MB
Number	TB	GLS	NL	FA	VL	MB	ET	HF	EN
	22.2	24.9	0.8	44.8	60.1	11.1	9.3	16.0	7.0
TTU 21907	85.0	8.0	19.0	15.0	46.1	24.6	2.0	38.9	11.2
	22.9	24.6	1.2	46.1	60.4	11.2	9.4	15.0	6.8
TTU 21906	85.0	10.0	17.0	15.0	43.7	25.2	1.9	37.3	11.3
	22.2	25.2	1.1	43.7	59.8	11.3	9.4	15.0	7.3
TTU 21905	82.0	10.0	19.0	16.0	47.2	25.9	2.2	40.5	11.2
	23.6	25.9	1.1	47.2	56.1	11.2	9.9	16.0	7.3
TTU 21904	83.0	9.0	18.0	15.0	46.0	26.2	2.2	38.1	11.6
	22.3	26.2	1.1	46.0	56.8	11.6	10.1	15.0	7.5
TTU 21903	84.0	11.0	19.0	15.0	46.6	25.6	1.6	39.9	11.7
	23.5	25.6	1.1	46.6	58.4	11.7	9.8	15.0	7.3
TTU 21902	82.0	10.0	19.0	14.0	45.9	25.5	1.4	37.7	11.4
	21.5	25.5	0.9	45.9	56.5	11.4	9.8	14.0	7.3
TTU 21901	82.0	10.0	19.0	15.0	46.7	25.8	1.8	39.9	11.4
	23.6	25.8	0.8	46.7	56.2	11.4	9.5	15.0	7.7
TTU 21925	72.0	9.0	17.0	14.0	45.6	25.0	2.2	39.0	11.1
	21.8	25.0	1.2	45.6	47.0	11.1	9.8	14.0	7.4

TTU—The Museum, Texas Tech University; TCWC—Texas Cooperative Wildlife Collection, Texas A&M University; TTL—total length; TL—tail length; EL—ear length; HF—hind foot length; FA—forearm length; GLS—greatest length of skull; CL—calcar-leg width; EN—distance from lacrimal canal to anterior margin of nasals; ND5—length of metacarpal of digit five; MB—mastoidal breadth; TB—tibia length; ML—width of maxilla at first incisors; VL—vertebral length; ET—distance from anterior margin of auditory meatus to lacrimal canal.

APPENDIX III

Matrices of Distance Values

Brachyphylla—1
Diphylla—2
Desmodus—3
Diaemus—4
Erophylla—5
Glossophaga—6
Monophyllus plethodon—7
Monophyllus redmani—8
Phyllonycteris—9

M-statistic untransformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	4.066	2.844	3.332	4.707	7.509	5.757	7.905	3.895
2	4.795	—	1.262	0.989	2.052	4.153	2.777	4.548	1.566
3	4.028	1.686	—	1.245	2.437	4.699	3.244	5.095	2.057
4	4.250	1.514	1.190	—	1.930	4.657	2.913	5.053	1.435
5	6.187	3.382	2.971	2.789	—	2.966	1.251	3.362	1.410
6	8.418	4.509	5.710	5.010	3.760	—	1.752	0.935	4.053
7	7.343	3.948	4.075	3.712	1.450	2.333	—	2.148	2.301
8	9.332	5.475	6.172	5.667	4.165	1.405	2.738	—	4.448
9	5.512	3.367	2.937	2.713	1.158	4.299	2.377	4.704	—

M-statistic untransformed bat measurements

M-statistic ratio transformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	1.476	1.351	1.147	1.099	0.926	1.199	0.805	1.273
2	1.674	—	0.867	0.847	1.691	2.152	1.997	1.501	1.352
3	1.405	1.394	—	1.248	1.602	2.149	2.020	1.343	1.622
4	1.017	1.384	1.126	—	1.450	1.776	1.856	1.193	1.173
5	1.717	2.939	2.461	2.438	—	0.987	0.701	0.679	1.152
6	2.206	2.847	3.487	2.972	1.802	—	0.822	1.004	1.435
7	2.188	3.456	3.278	2.955	0.953	1.768	—	0.867	1.049
8	1.689	2.088	2.671	2.050	1.466	1.302	1.705	—	1.273
9	1.761	3.079	2.542	2.577	1.042	1.486	1.340	1.482	—

M-statistic ratio transformed bat measurements

M-statistic log transformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	3.460	2.368	2.867	4.053	7.373	5.335	7.817	3.356
2	4.399	—	1.113	0.950	2.065	4.553	2.928	4.998	1.526
3	3.715	1.671	—	1.180	2.406	5.025	3.323	5.470	2.013
4	3.878	1.489	1.214	—	1.924	4.947	2.991	5.392	1.486
5	5.535	3.272	2.797	2.644	—	3.380	1.376	3.825	1.322
6	8.435	5.088	6.291	5.551	4.042	—	2.038	1.158	4.426
7	6.864	4.037	4.138	3.779	1.619	2.444	—	2.482	2.388
8	9.459	6.119	6.871	6.327	4.659	1.665	3.061	—	4.871
9	5.170	3.533	3.042	2.887	1.134	4.865	2.571	5.482	—

M-statistic log transformed bat measurements

Appendix III.—*Continued.*

D² untransformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	2.293	1.286	1.288	2.298	5.000	3.604	5.678	2.095
2	3.251	—	0.369	0.271	1.279	2.314	1.684	2.611	6.994
3	2.859	0.572	—	0.379	1.242	3.088	2.118	3.266	1.064
4	1.865	0.466	0.507	—	1.179	2.516	1.740	3.062	0.510
5	2.709	1.644	1.995	1.398	—	0.737	0.273	0.856	0.513
6	5.433	2.288	3.941	2.660	1.127	—	0.186	0.185	1.223
7	3.976	2.334	3.225	2.160	0.326	0.463	—	0.399	0.649
8	6.532	2.191	3.364	2.788	1.139	0.460	0.675	—	1.696
9	1.857	1.986	2.100	1.125	0.393	1.629	0.632	2.041	—

D² untransformed bat measurements

D² ratio transformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	1.840	0.951	0.989	2.106	4.823	3.516	5.467	1.862
2	2.710	—	0.349	0.263	1.293	2.645	1.819	2.934	0.687
3	2.284	0.565	—	0.357	1.198	3.285	2.170	3.399	1.000
4	1.490	0.455	0.492	—	1.246	2.774	1.909	3.370	0.534
5	2.360	1.762	2.073	1.481	—	0.786	0.289	0.841	0.512
6	5.628	3.246	5.144	3.564	1.490	—	0.201	0.266	1.340
7	3.849	2.736	3.639	2.514	0.392	0.601	—	0.372	0.707
8	6.005	2.874	4.149	3.316	1.128	0.559	0.530	—	1.901
9	1.716	1.961	2.053	1.146	0.341	1.964	0.678	1.910	—

D² ratio transformed bat measurements

D² log transformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	1.693	0.949	0.910	2.083	5.553	3.632	6.429	1.819
2	2.888	—	0.315	0.239	1.367	3.132	1.977	3.639	1.673
3	2.482	0.583	—	0.365	1.353	4.002	2.444	4.360	1.077
4	1.505	0.473	0.556	—	1.299	3.274	2.034	4.091	0.527
5	2.223	1.496	1.765	1.168	—	1.083	0.333	1.265	0.527
6	5.790	3.171	5.068	3.399	1.527	—	2.941	0.282	1.590
7	3.696	2.489	3.406	2.184	0.437	0.537	—	0.562	0.739
8	7.091	2.986	4.452	3.669	1.620	0.615	0.898	—	2.246
9	1.694	2.273	2.123	1.220	0.412	2.415	0.836	2.940	—

D² log transformed bat measurements

Appendix III.—*Continued.*

Euclidean untransformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	8.021	6.696	6.825	10.567	17.861	13.057	18.669	7.639
2	8.654	—	1.325	1.200	3.518	10.137	5.398	10.883	1.057
3	6.230	2.867	—	0.163	4.469	11.387	6.592	12.155	1.087
4	7.545	1.566	1.382	—	4.307	11.234	6.435	11.999	1.152
5	11.608	5.980	6.045	5.433	—	7.342	2.865	8.181	3.182
6	17.022	9.233	10.867	9.707	6.110	—	4.845	0.883	10.262
7	13.971	7.390	8.144	7.283	2.459	3.811	—	5.659	5.426
8	18.892	11.064	12.741	11.577	7.836	1.874	5.433	—	11.052
9	10.073	2.078	4.844	4.542	2.634	7.680	4.082	9.437	—

Euclidean untransformed bat measurements

Euclidean ratio transformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	3.368	3.710	2.043	3.440	4.763	4.729	3.298	2.174
2	2.014	—	1.038	2.324	4.791	7.840	6.586	5.314	3.390
3	2.690	1.121	—	2.097	5.689	8.398	7.453	5.794	4.224
4	2.180	0.909	1.989	—	5.044	6.777	6.582	4.146	3.547
5	5.800	7.183	8.406	7.782	—	4.220	1.815	3.017	1.520
6	7.895	9.696	10.568	9.337	3.621	—	3.332	2.637	4.770
7	8.645	10.649	11.258	10.574	2.852	3.416	—	3.457	3.229
8	2.927	7.403	8.314	6.993	3.270	2.375	4.774	—	2.705
9	5.628	7.640	8.210	7.635	0.271	3.877	3.056	3.415	—

Euclidean ratio transformed bat measurements

Euclidean log transformed frog measurements

	1	2	3	4	5	6	7	8	9
1	—	7.262	6.172	6.285	9.096	17.601	12.008	18.678	6.371
2	7.519	—	1.097	0.989	3.357	10.889	5.505	11.820	1.745
3	4.962	2.812	—	0.290	4.005	7.026	6.225	12.869	1.539
4	6.352	1.458	1.438	—	3.725	11.691	6.202	12.663	1.254
5	9.882	5.426	5.596	4.985	—	8.523	2.956	9.643	2.890
6	16.482	10.028	11.683	10.526	6.775	—	5.593	1.293	11.263
7	12.547	7.109	8.020	7.125	2.724	4.278	—	6.690	5.678
8	18.510	11.886	13.675	12.477	8.996	2.061	6.321	—	12.315
9	8.684	5.630	4.957	4.778	1.641	8.525	4.259	10.576	—

Euclidean log transformed bat measurements

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REVISION OF THE WIND RIVER FAUNAS, EARLY EOCENE OF CENTRAL WYOMING. PART 7. REVISION OF *DIACODEXIS* (MAMMALIA, ARTIODACTYLA)

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ABSTRACT

Four species of *Diacodexis* occur in the early and middle Eocene of western North America—*D. secans* (including synonyms *D. laticuneus, D. olseni, D. metsiacus, D. brachystomus*) and new species *D. woltonensis, D. minutus,* and *D. gracilis. D. secans* is divided into four informal, temporally successive lineage segments (*D. s.-primus, D. s.-metsiacus, D. s.-kelleyi, D. s.-secans*) to reflect anagenetic change in derived morphologic features in this single evolutionary lineage and species from its Sandcouleean (earliest Wasatchian) through Blacksforkian (middle Bridgerian) occurrence. Other diacodexeines and related groups arose from *D. secans* at different times in its anagenetic history—*D. gracilis* in the Graybullian from lineage segment *D. s.-metsiacus*; *D. woltonensis* and *D. minutus* in the Lysitean or Lostcabinian from *D. s.-kelleyi*; the *Wasatchia-Bunophorus* clade in the Sandcouleean from *D. s.-primus*; Leptochoeridae in the Gardnerbuttean (earliest Bridgerian) from *D. s.-secans*; and Antiacodontidae and Homacodontidae in the late Graybullian or early Lysitean from a *D. s.-metsiacus* sister group, Artiodactyla sp. A.

Evolutionary change (both anagenesis and cladogenesis) among these artiodactyls appears to have been gradual, chronoclinal, and mosaic, involving an increase in the degree

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[1] Equal authorship, as in all previous and forthcoming co-authored contributions to this series.

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of expression and frequency of occurrence of derived morphologic features, with canalization in single lineages and branching taxa. None of the apomorphic features are dichotomous; rather, they show normally distributed, continuous variation within species and overlap between species. Cladistic taxonomy cannot reflect such patterns. Different taxomonic treatments of anagenetic change within a single evolutionary lineage can result artificially in different apparent evolutionary patterns. Although the name *Diacodexis secans* represents "taxonomic stasis," it is emphatically not an indication of evolutionary stasis in the species *Diacodexis secans*. Similarly, neither the recognition nor naming of species different from *D. secans* implies a punctuated origin of or stasis in those species.

INTRODUCTION

Artiodactyls are among the most common small and medium-sized fossil mammals in the early and middle Eocene of North America. Since their last major revision (Sinclair, 1914), new and much larger collections of these early artiodactyls have been recovered from Wasatchian through Bridgerian horizons in the western interior, including the Wind River Basin. The new material warrants and allows a complete reevaluation of the diversity, systematics and evolutionary relationships of early artiodactyls.

For example, study of the Wind River Formation artiodactyls indicates the ocurrence of 13 species in seven genera—a much greater diversity of artiodactyls than hitherto recorded from the Wind River Formation or deposits of equivalent age. Of these taxa, three are new (two species of *Diacodexis*, one of *Homacodon*) and four represent new records for the Wind River Formation—*Hexacodus, Homacodon, Helohyus, Antiacodon pygmaeus*. The systematics and relationships of all North American species of *Diacodexis* are treated here. Other artiodactyl taxa—"*D. chacensis*," *Wasatchia, Bunophorus*, homacodontids, antiacodontids, leptochoerids—will be discussed elsewhere (Krishtalka and Stucky, manuscript; Stucky and Krishtalka, manuscript).

Eight North American species of *Diacodexis* have been named, all of which have had a tortuous taxonomic history. The type species, *D. laticuneus*, was originally referred to *Phenacodus* (Cope, 1882*a*) several months before Cope (1882*b*) named *Diacodexis*. The type specimen (AMNH 4202: P^{2-4}, M^{1-3}, M_3) is a composite: the upper premolars (now apparently lost) belong to *Hyracotherium* and the upper molars to *Hyopsodus powellianus*; only the M_3 represents *D. laticuneus* (see Matthew, 1899; Sinclair, 1914).

D. chacensis, D. secans, D. metsiacus, and *D. nuptus* were originally identified as species of *Pantolestes* (Cope, 1875, 1881, 1882*a*) and later referred to *Trigonolestes* (Matthew, 1899) and *Diacodexis* (=*Trigonolestes*, Sinclair, 1914).

D. brachystomus, originally assigned to *Mioclaenus* (Cope, 1882*a*), was transferred to *Pantolestes* and then *Trigonolestes* by Cope (1884,

1894) and to *Diacodexis* by Sinclair (1914), who, in the same study, also named *D. olseni* and *D. robustus.*

Sinclair (1914) synonymized *D. brachystomus* and *D. metsiacus* with *D. chacensis,* an action later questioned by Gazin (1952). Guthrie (1967) referred *D. nuptus* to *Cynodontomys* and, following Gazin (1952), recognized *D. metsiacus* (including *D. brachystomus* and *D. laticuneus*), *D. chacensis, D. secans, D. robustus,* and, tentatively, *D. olseni* as valid species of *Diacodexis.* In 1971, Guthrie synonymized *D. olseni* with *D. secans.* In the midst of this taxonomic shuffling, two type specimens—those of *D. metsiacus* and *D. chacensis*—were apparently lost or mislaid.

In the Wind River Basin, the taxonomic history of *Diacodexis* begins with E. D. Cope's (1881) description of *Pantolestes secans* from the Wind River Formation. Later, Sinclair (1914) named *Diacodexis olseni* from a single lower jaw from Davis Ranch (=Sullivan Ranch; CM loc. 34), a locality in the upper part of the Lost Cabin Member, Wind River Formation; Van Houten (1945) added *Diacodexis chacensis* to the fauna from this member. White (1952) recorded *D. olseni* from Wind River deposits in the Boysen Reservoir area, and Kelley and Wood (1954) reported *D. chacensis* from the Lysite Member. Guthrie (1967, 1971) listed the presence of *D. metsiacus* in the Lysite Member and two species of *Diacodexis, D. metsiacus* and *D. secans* (including *D. olseni*), in the Lost Cabin Member.

Since 1971, field parties from the Carnegie Museum of Natural History and the University of Colorado have greatly increased the collection of artiodactyls from many localities in the Lysite and Lost Cabin members and Red Creek facies of the Wind River Formation. Most of these localities can be correlated lithostratigraphically and biostratigraphically; they range in age from the middle and late Wasatchian (Lysitean-Lostcabinian) to the earliest Bridgerian (Gardnerbuttean).

Our study of Eocene *Diacodexis* indicates that four species warrant recognition, of which three are new—*D. secans* (including *D. brachystomus, D. olseni, D. metsiacus,* and *D. laticuneus*) and new species *D. minutus, D. woltonensis,* and *D. gracilis.* A number of specimens assigned below to Artiodactyla sp. A and sp. B may eventually prove to represent a new species of *Diacodexis* or a new genus. In either case, they appear to be basal to the radiation of homacodontid and antiacodontid artiodactyls. *D. chacensis* is referred elsewhere to a new genus (Krishtalka and Stucky, manuscript), and *D. robustus* to *Wasatchia* (Stucky and Krishtalka, manuscript). *D. nuptus* is a species of *Arctodontomys,* a microsyopid (Guthrie, 1967; Gunnell, 1985).

Among the four North American species of *Diacodexis, D. secans* is by far the most common and longest lived, ranging from the Sandcouleean (earliest Wasatchian, 54.5 ma) to the Blacksforkian (middle Bridgerian, 50 ma) in the western interior. Its first occurrence, in part, marks the onset of the Wasatchian (Rose, 1981; West et al., in press). *D. woltonensis* is limited in known occurrence to the Lostcabinian of the Wind River Formation, Wyoming; *D. minutus* to the Lostcabinian and Gardnerbuttean of the Wind River Formation and the Lostcabinian of the Huerfano Formation, Colorado; *D. gracilis* to the late Graybullian of the Willwood Formation, Wyoming. Artiodactyla sp. A and sp. B occur in the late Graybullian and/or early Lysitean of Colorado (Debeque Formation) and New Mexico (San Jose Formation). Two species of *Diacodexis* have been reported from Europe (*D. gazini, D. varleti*; Sudre et al., 1983) and one from Asia (*D. pakistanensis*; Thewissen et al., 1983).

Diacodexis, specifically *D. secans* appears to be the most primitive known artiodactyl in dental morphology, and, as discussed below, is basal to the radiation of all other artiodactyls, a conclusion based on the range of morphological variation and anagenetic change in derived features in this Sandcouleean through Blacksforkian species-lineage.

One crucial point that has emerged from this study is the implication for systematics and evolutionary theory of variation within and among samples from single and disparate localities. In paleontological practice, morphology guides the allocation of specimens to individual species. But, the translation of the range and limits of variation into these paleontological species, either statistically or subjectively, can result in different reconstructions of evolutionary patterns. Very simply, taxonomic decisions regarding the composition of paleontological species can artificially determine the resultant evolutionary pattern and mode.

Recognition of paleontological species at a single locality and from a single horizon (lithosympatry; see Stucky, 1984) is usually straightforward: there is little or no morphological overlap between them, regardless of the number of species present, and each species exhibits a normally distributed variation.

However, complications arise when stratigraphically and geographically disjuct samples are added to the analysis and show varying degrees of morphological overlap in derived features with one or more species. Such diachronic or spatially separated samples are never morphologically congruent with one another to our knowledge. Grouping of these samples into paleontological species can involve several alternatives; it is especially difficult when the derived and overlapping features are not dichotomous, that is, not either present or absent, but merely evolving traits along several morphoclines.

This is exemplified by most samples of *Diacodexis,* which show a combination of continuous variation over geologic time and across geographic space, with apparently continuous and directional change in the frequency and degree of expression of derived morphological features. Subdivision of such samples into a series of overlapping species (for example, Gingerich's 1976, 1979 treatment of notharctines)—to reflect this change as well as stratigraphic integrity—can imply a series of anagenetic speciation events. Alternatively, inclusion of such samples into one "evolutionary species" can *a priori* imply stasis and punctuationalism in some quarters (for example, Stanley, 1982, with regard to Schankler's, 1980, *D. metsiacus* in the Bighorn Basin). Clearly, in these instances, theoretical notions of evolutionary patterns can bias and determine taxonomic decisions; the reverse is also true—the composition and recognition of paleontological species can determine the evolutionary pattern.

The static and typological nature of Linnaean nomenclature when applied to a diachronic fossil record compounds this problem, especially when that record preserves temporally continuous morphologic change in derived features. Linnaean nomenclature cannot adequately reflect significant and continuous evolutionary change in a single lineage through time. Neither can cladograms. Cladistic conventions, which by definition are dichotomous, non-temporal and non-geographic, ignore this problem and assume that such anagenetic change is either minor, insignificant, or non-existent. However, a good fossil record, such as that of *Diacodexis,* flies major anagenetic change in the face of artificial conventions, as does a good Recent record of clinal change (Simpson, 1953; Gingerich, 1976, 1979; Wolpoff, 1985; Van Valen, 1982; Barnosky, 1982; Rose and Bown, 1984; Krishtalka and Stucky, 1983*a,* 1983*b*; Stucky and Krishtalka, 1983; Harris and White, 1979; Cooke, 1978; Endler, 1977; Rensch, 1960; Vrba, 1984; Chaline and Mein, 1979; Brunet and Heintz, 1982; Fahlbusch, 1983). Whatever the taxonomic solution adopted, the recognition and description of the pattern of morphologic variation through time and space, both within and among species, can untie this Gordian Knot and give a truer indication of evolutionary patterns than can ever be reflected by taxonomic nomenclature.

Our solution to the problem of translating anagenetic change in derived features in temporally disjunct samples (either stepped or continuous morphoclines; Endler, 1977) into taxonomic units is threefold: (1) We group such samples into one species, which is also an evolutionary lineage; such species-lineages are examples of anagenetic and phyletic evolution through time, with no increase in diversity. For this reason we choose not to divide such lineages into separate species. However, although the use of one species name to denote an evolutionary lineage may be "nomenclatorial stasis," it emphatically does not imply evolutionary stasis. Theoreticians who assay the fossil record for patterns of stasis by simply counting numbers of named species and their geologic ranges (for example, Stanley, 1982) and disregard the morphologic patterns among and within these species are missing the evolutionary boat. This is not to say that stasis does not occur; it does, sometimes alongside gradualism (Krishtalka and Stucky, 1983*a*, 1983*b*; Williamson, 1981; West, 1979; Vrba, 1984).

(2) Evolving morphoclines (of especially non-meristic traits as well as size) are the hallmark of paleontological species-lineages. To reflect such change, we divide a species-lineage into *informal* lineage segments, which are temporally successive and morphologically overlapping units here designated by a hyphenated trinomial. Although the lineage segments and their names are informal, we follow nomenclatorial convention in using the available name of a synonymized species for a particular lineage segment if the type specimen of that species falls within the morphologic range of that lineage segment. For example, the species *Diacodexis secans* includes the informal lineage segments *D. s.-metsiacus* (contains cotype of *D. metsiacus* and holotype of *D. brachystomus*) and *D. s.-secans* (contains holotypes of *D. secans, D. olseni, D. laticuneus*), as well as *D. s.-primus* and *D. s.-kelleyi,* two new informal names. Obviously, assignment of individual specimens to particular lineage segments is based on relative position within the morphocline; but it is, in part, arbitrary, given the degree of morphologic overlap between temporally adjacent lineage segments. Clearly, a lineage segment cannot have invariant specializations that preclude its ancestral position with regard to descendant lineage segments. Lineage segments are, to us, preferable to "temporal subspecies." For one, subspecies are formal designations of spatial patterns within one species, whereas we intend lineage segments to be *informal* designations of specific temporal patterns within a species-lineage. For another, paleontological subspecies and the patterns they are invoked to reflect are usually ignored in the literature.

(3) We designate a diagnostic series of specimens (rather than one type specimen) to represent each lineage segment. This series encompasses the known range of variation and the degree of morphologic overlap with temporally adjacent lineage segments and other species. Holotypes represent formal taxa and, as such, do not apply to our informal lineage segments. Moreover, the use of holotypes detracts from the pattern of intrataxon variation by focusing attention on the morphological traits of a single specimen.

We recognize separate species (and cladogenetic events) where there is little or no morphologic overlap (in non-meristic traits and/or size) between geologically disjunct, penecontemporaneous, or lithosympatric samples, which themselves show continuous, normally distributed variation. Recognition of separate species reflects cladogenetic events and an increase in diversity, but is not, in itself, evidence of a particular evolutionary tempo or mode.

Also, it is apparent that "paraphyletic" taxa, in the nomenclatorial sense, are real—different cladogenetic events can occur at different times from different lineage segments of an evolutionary species. For example, it appears that different taxa of artiodactyls—in hindsight, the most primitive members of originating suborders, families and subfamilies—arose at different times from different lineage segments of the single species *D. secans*. As such, some systematists would consider the genus *Diacodexis* and the species *D. secans* as "paraphyletic," a label that may sacrifice evolutionary reality for classificatory and nomenclatorial convenience. The evolution of the *D. secans* lineage segment *D. s.-secans* and *D. woltonensis* from lineage segment *D. s.-kelleyi*, and the evolution of *D. gracilis* and *D. s.-kelleyi* from *D. s.-metsiacus* fall in the same category. These taxa may be "paraphyletic" according to cladistic convention, but they more nearly reflect the morphological and evolutionary pattern of species as reconstructed from the fossil record rather than does any scheme based solely on nomenclatorial conventions and dichotomous characters (Van Valen, 1978).

Finally, size is only *one* trait that figures in our recognition of some of the species of *Diacodexis*, as well as in the apparent pattern of anagenetic change in the species-lineage *D. secans*. Non-meristic morphological features are as or more important, and comprise most of the criteria in the diagnoses of species and lineage segments. As such, our evolutionary conclusions are based on suites of derived morphological traits, only one of which is size.

The presence and relative strength of three features used here—pseudohypocone, postmetacristid, talonid notch—are, along with others, of major importance in the systematics of *Diacodexis* and require precise definition. The pseudohypocone, on upper molars, occurs on the postprotocrista immediately posterior and adjacent to the apex of the protocone. The postmetacristid is a crest that descends the posterolingual face of the protoconid on P_4 and that of the metaconid on the lower molars. The talonid notch occurs between the bases of the metaconid and entoconid on lower molars, where the talonid basin is deepest and opens lingually.

Abbreviations in text and tables are as follows: ACM, Amherst College Museum; AMNH, American Museum of Natural History; CM, Carnegie Museum of Natural History; PU, Princeton University; UCM, University of Colorado Museum; USGS, United States Geological Survey, Denver; UW, University of Wyoming; L, length; W, width; N, number; C. V., coefficient of variation; SD, standard deviation.

SYSTEMATICS

Family Diacodexeidae (Gazin, 1955), new rank[1]
Subfamily Diacodexeinae Gazin, 1955
Diacodexis Cope, 1882*b*

Diacodexis Cope, 1882*b*:1029.
Trigonolestes Cope, 1894:868.

Type species.—*Diacodexis secans* (Cope, 1881), including *D. laticuneus, D. brachystomus, D. metsiacus, D. olseni.*

Included species.—Type species and *D. minutus, D. woltonensis, D. gracilis, D. gazini, D. varleti, D. pakistanensis.*

Known distribution.—Early to middle Eocene of North America; early Eocene of Europe and Asia.

Diacodexis secans (Cope, 1881)

Pantolestes secans Cope, 1881:187; 1884:725, plate 25a.
Pantolestes metsiacus Cope, 1882*a*:149; 1884:719, plate 25e.
Phenacodus laticuneus Cope, 1882*a*:181.
Mioclaenus brachystomus Cope, 1882*a*:187.
Diacodexis laticuneus (Cope, 1882*a*), Cope, 1882*b*:1029; 1884:492, plate 25e; Sinclair, 1914:290.
Pantolestes brachystomus (Cope, 1882*a*), Cope, 1884:721, plate 23d.
Trigonolestes brachystomus (Cope, 1882*a*), Cope, 1894:868; Matthew, 1899:34.
Hyopsodus laticuneus (Cope, 1882*a*), Matthew, 1899:30, M_3 only.
Trigonolestes metsiacus (Cope, 1882*a*), Matthew, 1899:34.
Trigonolestes secans (Cope, 1881), Matthew, 1899:36.
Diacodexis chacensis (Cope, 1875), Sinclair, 1914:290, in part; Kelley and Wood, 1954: 364.
Diacodexis secans (Cope, 1881), Sinclair, 1914:290; Guthrie, 1971:85.
Diacodexis olseni Sinclair, 1914:292, fig. 26; White, 1952:202; Stucky, 1984:279.
Diacodexis metsiacus (Cope, 1882*a*), McKenna, 1960:121; Guthrie, 1967:49; Delson, 1971:357; Rose, 1982:621.
Diacodexis cf. *secans,* West, 1973:148.
Diacodexis cf. *metsiacus,* Bown, 1979:106, fig. 59c–e.
Diacodexis sp., Eaton, 1982:187, fig. 16E.

Holotype.—AMNH 4899, left and right P_4–M_3, from the Wind River Formation, Wind River Basin, Wyoming.

Included lineage segments.—*D. secans-primus, D. s.-metsiacus, D. s.-kelleyi, D. s.-secans.*

Diagnosis.—Larger than all penecontemporaneous species of *Diacodexis* and more robust than *D. gracilis, D. minutus* and Artiodactyla sp. A and sp. B, with more inflated molar protocones, metaconids and hypoconids. Additionally, differs from *D. gracilis* in having a less reduced and less medial paraconid on M_{1-3}, and more nearly square

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[1] *dexeos* is the genitive form of *dexis*; hence, Diacodexeidae.

M_{1-2}; M_{1-3} talonids more shallow and cusps more bunodont than in Artiodactyla sp. A and sp. B and *D. minutus*; M_{1-3} metaconids less inflated in proportion to tooth size than in *D. woltonensis*; M_{1-3} paraconids and paracristids more developed than in Artiodactyla sp. A and sp. B, paraconids and metaconids less elevated, entoconid lower than hypoconid and hypoconulid not lingually placed near entoconid.

Referred specimens and localities.—See listing below under individual lineage segments.

Known distribution.—Earliest Wasatchian through middle Bridgerian (Sandcouleean through Blacksforkian) of Wyoming and Colorado.

Discussion.—Our review of the types and other material of named species of *Diacodexis* indicates the following: (1) material from the early and middle Eocene previously identified as or allied to *D. secans, D. metsiacus, D. brachystomus, D. laticuneus, D. olseni,* and *D. chacensis* (in part) shows gradual temporal change with continuous overlap in the frequency and degree of expression of derived morphological features, as detailed below. This lineage represents a single evolutionary species, *D. secans,* which is a senior synonym of *D. metsiacus, D. brachystomus, D. laticuneus,* and *D. olseni.* Sinclair (1914), Gazin (1952), and Guthrie (1967, 1971) reached similar conclusions.

(2) *D. secans* is a Sandcouleean through Blacksforkian evolutionary lineage in which we recognize four successive and informal lineage segments—*D. secans-primus* (Sandcouleean–early Graybullian), *D. s.-metsiacus* (late Graybullian), *D. s.-kelleyi* (Lysitean–?early Lostcabinian) and *D. s.-secans* (Lostcabinian–Blacksforkian). Thus, *D. secans* includes Lysitean through Gardnerbuttean samples of *Diacodexis* from the Wind River Formation that were previously assigned to *D. secans, D. metsiacus,* and *D. olseni* (Sinclair, 1914; White, 1952; Guthrie, 1967, 1971; Stucky, 1982), as well as non-Wind River Formation material previously referred to or allied with *D. metsiacus* (McKenna, 1960; Delson, 1971; Bown, 1979; Rose, 1982), *D. secans* (West, 1973), and *D. chacensis* (Sinclair, 1914).

(3) *D. chacensis,* redefined on topotypic material, is referred elsewhere (Krishtalka and Stucky, manuscript) to a new genus.

(4) AMNH 17560, a lower jaw with P_4–M_2 from one of the Gardnerbuttean Huerfano localities, which was identified by Robinson (1966) as *Diacodexis* sp. cf. *D. secans,* bears the derived morphology of leptochoerids, and represents the earliest known occurrence of that family. This new genus and species will be described elsewhere.

Major anagenetic trends (or temporal morphoclines) between the successive lineage segments in this species involve: (1) increase in size, robusticity and bunodonty of $P^2/_2$–$M^3/_3$; (2) elongation of $P^2/_2$–$P^4/_4$ relative to the molars; (3) stronger protocone and metacone on P^3; greater asymmetry of P^3, with protocone occurring more posteriorly;

development on P_4 of a postmetacristid alongside the cristid obliqua; (4) development of a deep talonid notch and a strong postmetacristid on the lower molars; (5) inflation of molar metaconids, hypoconids, and protocones, with consequent weakening or obliteration of upper molar protocristae, conulecristae, and pseudohypocones; (6) some reduction and slight medial shift of the molar paraconid; (7) isolation of the hypoconulid on M_3 and shortening of the hypoconulid lobe.

These trends appear to have evolved as a morphological nexus, with increasing canalization (by shifts in the frequency and degree of expression) and correlation of character states through time. For example, the postmetacristid and talonid notch on M_{1-3} are virtually absent in *D. s.-primus,* infrequent and weak (when present) in *D. s.-metsiacus,* more frequent and moderately developed (when present) in *D. s.-kelleyi,* and almost always present and strongly developed in *D. s.-secans.* Correlated with this temporal morphocline is the gradual increase in bunodonty (point 5 above) and the other trends cited above.

As such, there is significant and apparently continuous morphologic overlap between temporally adjacent segments of this lineage, with moderate shifts in the mean values and frequencies of character states. There is virtually no overlap between end members (*D. s.-primus, D. s.-secans*), which would be considered separate species if found in lithosympatry (they are not), and which indicates major anagenetic change rather than stasis. Each of the lineage segments, in turn, exhibits continuous variation in the character states listed above. Also, samples from discrete horizons, localities or stratigraphic intervals referred to each lineage segment show normally distributed patterns of variation. Individual specimens in zones of overlap cannot be assigned with confidence to one or another lineage segment. The same holds for isolated teeth, especially M_1s.

D. secans is the oldest known species of artiodactyl in North America and its first appearance, along with that of other genera, marks the onset of the Wasatchian (Rose, 1981; West et al., in press). It occurs penecontemporaneously with *D. gracilis* and Artiodactyla sp. A and sp. B (late Graybullian–early Lysitean), *D. woltonensis* (Lostcabinian), and *D. minutus* (Lostcabinian–Gardnerbuttean). As discussed elsewhere (Stucky and Krishtalka, manuscript), other diacodexeids (*Wasatchia, Bunophorus*), antiacodontids, homacodontids and leptochoerids (*sensu stricto,* that is, *Leptochoerus, Stibarus, Ibarus*) appear to have arisen through cladogenesis from different lineage segments of *D. secans* and are most closely related to this species.

Lineage Segment *Diacodexis secans-secans*
(Figs. 1–2; Tables 1–4)

Diagnosis.—Largest (mean size) and most robust lineage segment of *D. secans,* with P_2 and $P^3/_3$ more elongate, P^3protocone more posterior,

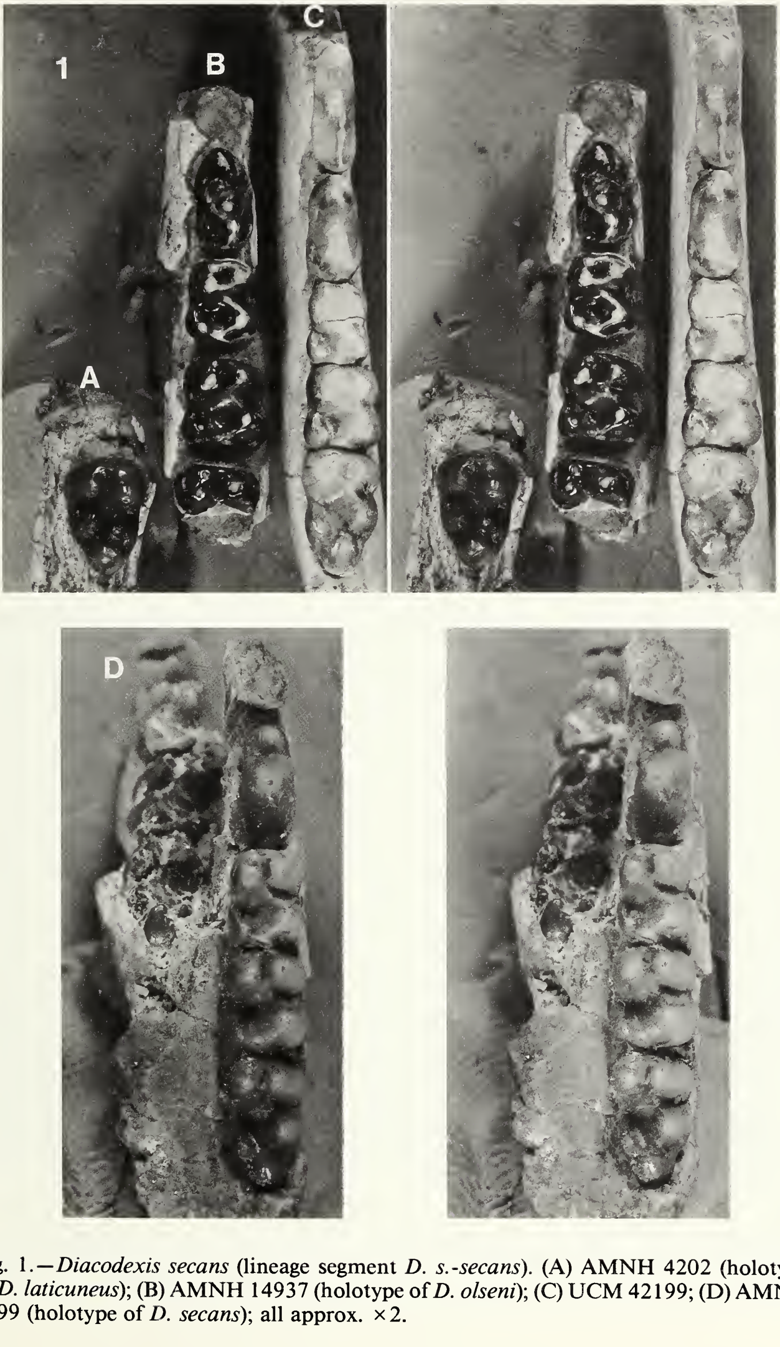


Fig. 1.—*Diacodexis secans* (lineage segment *D. s.-secans*). (A) AMNH 4202 (holotype of *D. laticuneus*); (B) AMNH 14937 (holotype of *D. olseni*); (C) UCM 42199; (D) AMNH 4899 (holotype of *D. secans*); all approx. ×2.

P_3 longer than M_3, molars more bunodont, M_{1-2} more nearly square, more inflated molar protocones, conules, protoconids, metaconids and hypoconids, and less distinct protocristae, pseudohypocones and conulecristae; M_{1-3} with stronger postmetacristid and deeper talonid notch; $P^4/_4$, $M^1/_1$ proportionately broader and more robust.

Diagnostic series.—AMNH 4899 (holotype of *D. secans*), AMNH 4202 (holotype of *D. laticuneus*), AMNH 14937 (holotype of *D. olseni*); CM 42082, 43736, 22504, 22507, 43476, 35780, 21017, 22503, 44849, 39880, 43717; UCM 42199; PU 20599.

Referred specimens.—CM 21017, 21020, 21025, 21063, 21104, 21135–21138, 21140, 21213, 21217, 21228, 22503, 22504, 22506–22511, 22532, 27455, 27480, 30891, 30944–30948, 30950, 30951, 35732, 35771, 35772, 35774–35784, 35816, 36439, 36441, 36444, 36445, 36931, 36934, 37299, 37300, 37302, 37304, 37307, 37308, 40764, 40770, 40776, 40778–40781, 40784, 42073, 42074, 42079, 42080, 42082, 42087, 42096, 42097, 42125, 43469, 43475–43477, 43479, 43711, 43717, 43730–43737, 43744, 44846, 44849, 44908–44911, 51636, 55133, 55140, 55141, 55143, 55151, 55156, 55158, 55160, 55162, 55164–55169, 55351, 55353, 55356–55360, 55362, 55366, 55368; UCM 42199, 44906, 44341, 46508, 46582, 46809, 46811, 47026; AMNH 4202 (holotype of *D. laticuneus*), AMNH 14937 (holotype of *D. olseni*); PU 20598, 20599, 20800, 22317, 22471.

Localities.—CM locs. 91, 92, 99, 1039, 1040, 1041, 1042, 1046, 1077, 1084, 1534; PU loc. Alkali Creek (all Lostcabinian, Lost Cabin Mbr., Wind River Fm.). UCM locs. 80062, 81008 (Lostcabinian, Red Creek Facies, Wind River Fm.). CM loc. 216 (Lostcabinian, Wasatch Fm.). CM loc. 90 (Lostcabinian or Gardnerbuttean, Lost Cabin Mbr., Wind River Fm.). CM locs. 34, 1036, 1038; UCM locs. 81010, 79041 (all Gardnerbuttean, Lost Cabin Mbr., Wind River Fm.). CM loc. 1096 (Blacksforkian, Bridger Fm.); all in Wyoming.

Known distribution.—Late Wasatchian through earliest Bridgerian (Lostcabinian through Gardnerbuttean)—Wind River Basin (Wind River Fm.); late Wasatchian (Lysitean or Lostcabinian)—Bighorn Basin (?Willwood Fm.); late Wasatchian to middle Bridgerian (Lostcabinian—Blacksforkian)—Green River Basin (Wasatch Fm., Bridger Fm.); all in Wyoming.

Description.—Teeth anterior to $P^2/_2$ are unknown. P_2 and P_3 are elongate and narrow in occlusal view, and triangular in side view. The central, tall protoconid leans posteriorly and is joined by sharp cristids to a small anterobasal paraconid and a posterobasal cuspule (?hypoconulid). The roots of both premolars diverge ventrally. P_3 is longer than P_2 and has more nearly rectangular occlusal outline, a stronger paraconid and lower protoconid. The posterior crest (?cristid obliqua) to the posterobasal cuspule bears a hypoconid below the protoconid. A poorly developed cingulid rings the posterior one-quarter of the crown. P_3 is longer than any of the other premolars and molars.

P_4 is shorter, wider and more robust than P_3, but is longer and as wide as M_1. In occlusal view it is rectangular to ovoid and wider posteriorly than anteriorly. The basal cingulid is well-developed except at the lingual and labial base of the protoconid. The anterobasal paraconid can be single or double. The cristid obliqua and hypoconid are variably developed but are always stronger than on P_3. On many P_4s a postmetacristid

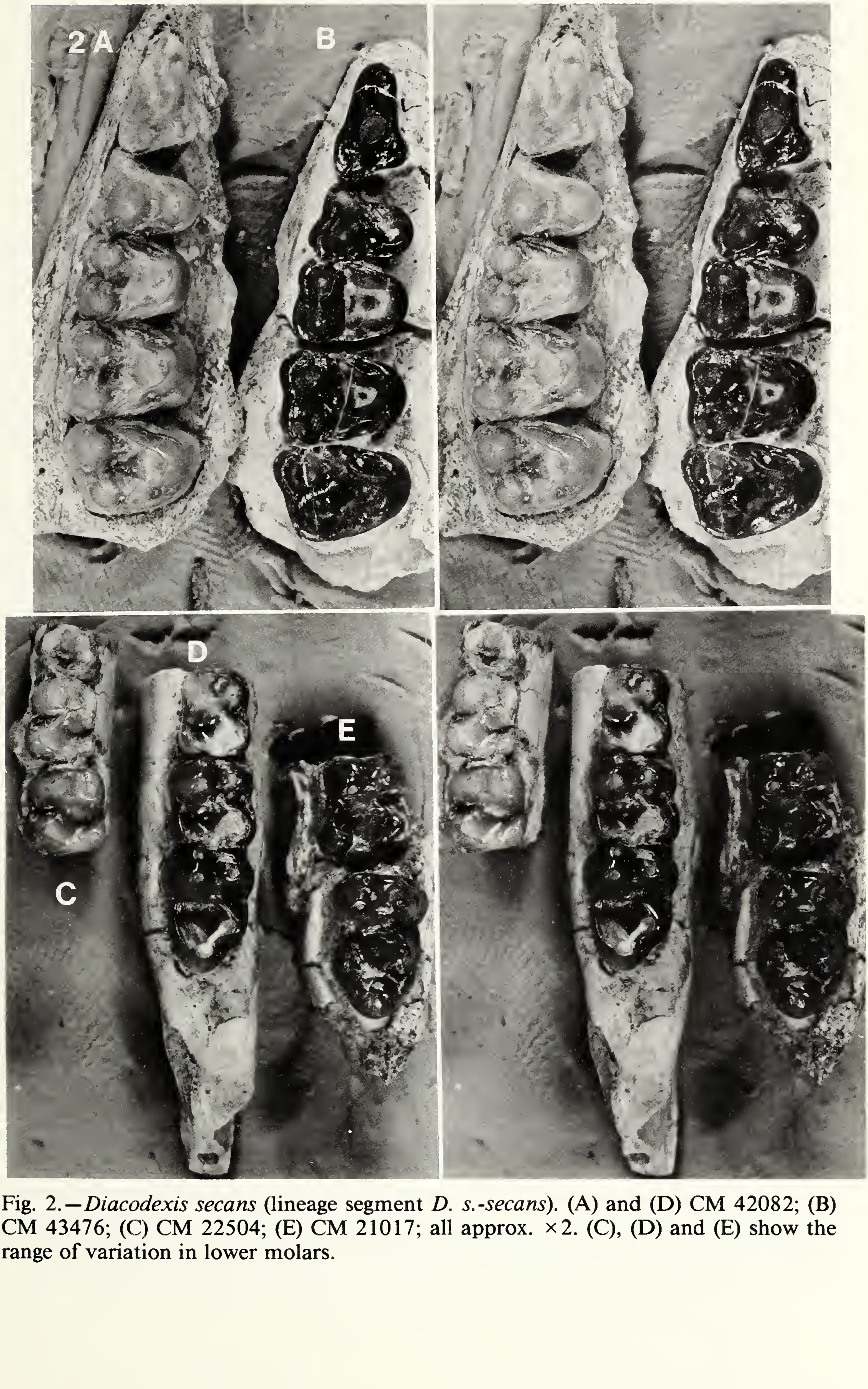


Fig. 2.—*Diacodexis secans* (lineage segment *D. s.-secans*). (A) and (D) CM 42082; (B) CM 43476; (C) CM 22504; (E) CM 21017; all approx. ×2. (C), (D) and (E) show the range of variation in lower molars.

runs parallel and labial to the cristid obliqua from the protoconid to just above the talonid basin. Posteriorly, the basal cingulid may be crenulate, with several accessory cuspules.

M_1 and especially M_2 are square in occlusal view, whereas M_3 is more rectangular and tapers posteriorly. The lower molars are robust and bunodont; all of the major cusps are inflated at the base. The metaconid is somewhat larger and taller than the protoconid and bulges lingually. The paraconid, much smaller than the metaconid, lies anterior and slightly labial to the latter. Both cusps are conjoined, so that only their apices are distinct. The cristid obliqua meets the trigonid medially or, especially on M_1, just lingual to the mid-point. The hypoconid is larger and taller than the conical entoconid, which can be single, double or multicuspate, especially on M_3. The talonid basin opens lingually through a deep talonid notch, and a strong postmetacristid descends the posterolingual face of the metaconid to the notch. In some specimens the postmetacristid and pre-entocristid form a complete ridge that closes the talonid notch.

The talonids on M_{1-2} are broader than or as wide as the trigonids, and slightly lower than the latter. The hypoconulid, smaller and lower than the entoconid, occurs just lingual to the midline of the crown; a strong notch separates the two cusps. A ridge-like postcingulid descends from the apex of the hypoconulid along the posterior face of the hypoconid. On M_3 the talonid is narrower than the trigonid, and the hypoconulid and hypoconid are equal in size and height.

P^3 resembles an asymmetrical triangle in occlusal view, and is almost twice as long as it is wide. The crown is dominated by a tall, central paracone. The preparacrista runs directly anteriorly and ends in a basal parastyle. The postparacrista runs directly posteriorly and bears a small, conical metacone. A weak protocone, the lowest of the cusps, occurs directly lingual to the notch between the paracone and metacone. As such, the protocone is offset posteriorly; its distance from the parastyle is twice that to the tip of the metastylar salient.

Unlike P^3, P^4 and the upper molars are wider than long. P^4 bears a broad paracone labially, a smaller and lower protocone lingually, and a small parastylar wing. A strong cingulum runs around the base of the protocone.

M^{1-3} are robust and bunodont, with basally inflated cusps, especially the protocone. M^2 is larger than M^1 and more nearly square; M^3 varies in shape from trapezoidal to triangular. On M^{1-2} the paracone is slightly smaller than the metacone; both cusps are conical and joined by a shallow, anteroposteriorly directed centrocrista. The protocone is medial, and has a greatly expanded base, a long lingual slope, and a "pseudohypocone" bulge on its posterior face. Short protocristae extend to the metaconule and slightly smaller paraconule. Weak notches separate the conules from the protocone on some specimens. The external conulecristae are strong and reach the cingula, whereas the internal ones are either much weaker or virtually absent. The pre- and postcingula are broad and each bears a cuspule at a point adjacent to the labial face of the protocone. The ectocingulum is also well-developed and often crenulate. M^3 differs from M^{1-2} in having a smaller metacone than paracone and, on some specimens, a weak, medial swelling (?mesostyle) on the centrocrista.

Discussion.—D. s.-secans is the end member of the evolutionary lineage (and species) *D. secans.* As described in the diagnosis, its diagnostic and derived morphologic features differ in frequency and degree of expression from those of the other lineage segments in the species, and are apparently the result of anagenetic evolution from the latter. *D. s.-secans* overlaps to a significant degree in size and most morphological features with *D. s.-kelleyi,* its immediate temporal predecessor, and less so with the other two lineage segments (Tables 1, 2).

In the Wind River Basin, *D. s.-secans* occurs in lithosympatry with *D. woltonensis* at Lostcabinian localities and with *D. minutus* at Lostcabinian and Gardnerbuttean ones (Figs. 12, 13). A single Gardnerbuttean horizon (at CM loc. 34) has yielded the largest sample of *D. s.-secans,* which shows a normal distribution that overlaps very little with that of the lithosympatric *D. minutus.* The two smallest specimens of *D. s.-secans* (CM 22504, UCM 46509) closely resemble the two largest of *D. minutus* (CM 40769, 42072) in size and degree of cusp inflation, but are distinct in the greater expansion of the posterior wall of the metaconid. Variable features in the CM loc. 34 sample of *D. s.-secans* include: size, strength, and position of molar paraconids; development of postmetacristids, talonid notches, conulecristae, cingula, and cingular cuspules; strength and crennulation of the P_4 cingulid; presence of a P_4 postmetacristid. There is some morphologic overlap between a few specimens in this Gardnerbuttean sample (especially CM 22504) and Lostcabinian *D. woltonensis,* but there is no overlap between the latter and lithosympatric Lostcabinian samples of *D. s.-secans.*

D. s.-secans appears to be closely related to later leptochoerids (Stucky and Krishtalka, manuscript), and may have shared an immediate common ancestry with *D. minutus* and *D. woltonensis,* a tentative conclusion based on their common possession of the following derived features—M_{1-3} talonid short lingually; strong development of M_{1-3} postmetacristid and talonid notch. However, given the variation in these features (absent to fully developed), as well as their occurrence in *D. s.-metsiacus* and *D. s.-kelleyi* (albeit at a weaker condition and lower frequency), they could have evolved in parallel in *D. minutus, D. woltonensis,* and *D. s.-secans.*

This lineage segment includes the type specimens of *D. secans* and junior synonyms *D. laticuneus* and *D. olseni.* Although the holotypes bear distinctive characteristics, these features vary greatly within Lostcabinian and Gardnerbuttean samples. The holotype of *D. secans* is perhaps unique in its combination of a large paraconid on P_4, reduced molar paraconid, especially on M_2, reduced entoconid on M_{1-3}, and elongate hypoconulid lobe on M_3. The left molars, recently prepared, have a stronger entoconid than the right ones. Nonetheless, all of these features occur on specimens previously identified as *D. olseni* and *D. secans* (Guthrie, 1971); the continuous variation within the latter includes the morphology of the type M_3 of *D. laticuneus.*

The holotype of *D. olseni* comes from CM loc. 34 (Gardnerbuttean), but the exact ages of the other two type specimens are uncertain. Judging from the fauna that was originally collected with the type of *D. secans* (Cope, 1881), its age is either Lostcabinian or Gardnerbuttean. The type M_3 of *D. laticuneus* is probably late Wasatchian, given that the

Table 1.—*Summary statistics of lower dentitions of* Diacodexis secans *(lineage segments* Diacodexis secans-primus, D. secans-metsiacus, D. secans-kelleyi, D. secans-secans*)*, D. woltonensis, D. minutus, D. gracilis, *and Artiodactyla sp. A.*

Taxa and statistics	P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W
Diacodexis secans-secans										
Range	6.0–7.3	2.0–2.7	5.2–6.2	2.5–3.4	4.0–5.3	3.2–4.1	4.3–5.3	3.9–5.3	5.6–7.1	3.7–4.9
N	6	6	20	20	39	41	53	54	47	52
Mean	6.53	2.32	5.62	3.00	4.53	3.64	4.79	4.41	6.36	4.35
SD	0.50	0.23	0.25	0.27	0.22	0.22	0.26	0.27	0.37	0.27
C.V.	7.66	9.91	4.45	9.00	4.86	6.04	5.43	6.12	5.82	6.21
Skewness	0.59	0.42	0.50	0.04	0.49	0.15	0.18	0.63	−.22	0.12
Diacodexis secans-kelleyi										
Range	5.3–5.6	1.60	4.2–5.3	2.1–3.2	4.0–4.6	2.8–3.8	4.0–4.9	3.5–4.5	5.1–6.4	3.1–4.5
N	2	2	34	36	49	47	58	56	50	52
Mean	5.43	1.60	4.80	2.61	4.25	3.31	4.47	3.97	5.73	3.72
SD	—	—	0.30	0.22	0.16	0.22	0.23	0.26	0.30	0.26
C.V.	—	—	6.25	8.43	3.76	6.65	5.15	6.55	5.24	6.99
Skewness	—	—	0.01	0.27	0.43	−.03	0.02	−.01	−.09	0.30
Diacodexis secans-metsiacus										
Range	5.0–5.8	2.0–2.2	4.5–5.7	2.2–3.6	3.7–4.6	3.0–3.6	4.0–4.7	3.3–4.2	4.6–5.8	3.1–4.0
N	5	4	28	29	32	39	50	52	34	38
Mean	5.54	2.10	4.95	2.79	4.16	3.27	4.36	3.73	5.17	3.43
SD	0.33	0.12	0.28	0.33	0.16	0.17	0.19	0.24	0.28	0.21
C.V.	5.96	5.71	5.66	11.83	3.85	5.60	4.36	6.43	5.42	6.99
Skewness	−.96	—	0.45	1.00	−.23	0.08	−.15	−.04	−.02	0.23
Diacodexis secans-primus										
Range	4.7–5.0	1.7–2.0	4.2–5.0	2.1–2.9	3.8–4.3	2.9–3.4	4.0–5.0	3.5–4.2	5.0–6.7	3.5–4.1
N	4	5	18	19	20	25	40	41	39	39
Mean	4.85	1.84	4.61	2.46	4.07	3.17	4.51	3.89	5.83	3.75
SD	0.13	0.13	0.25	0.22	0.13	0.16	0.22	0.17	0.36	0.20
C.V.	2.68	7.07	5.42	8.94	3.19	5.05	4.88	4.37	6.17	5.33
Skewness	—	−.11	0.08	0.36	−.16	−.24	0.05	−.14	0.30	0.20

Table 1.—*Continued.*

Taxa and statistics	P_3		P_4		M_1		M_2		M_3	
	L	W	L	W	L	W	L	W	L	W
Diacodexis woltonensis										
Range		2.40	5.0–5.7	2.6–3.1	4.0–4.3	3.2–3.4	4.1–4.3	3.5–4.0	4.9–5.6	3.4–4.0
N		1	6	6	5	5	7	7	7	7
Mean		2.40	5.35	2.83	4.14	3.32	4.21	3.76	5.27	3.70
SD		—	0.27	0.22	0.13	0.08	0.07	0.16	0.26	0.23
C.V.		—	5.05	7.77	3.14	2.41	1.66	4.26	4.93	6.22
Skewness		—	−.10	0.44	−.11	−.34	−.13	−.01	0.15	−.26
Diacodexis minutus										
Range	5.0–5.4	1.7–2.0	4.1–5.0	2.0–2.8	3.6–4.4	2.6–3.5	3.7–4.4	3.1–3.6	4.5–5.4	2.9–3.6
N	3	3	23	23	27	27	34	34	26	27
Mean	5.20	1.83	4.56	2.47	3.85	3.06	4.02	3.40	4.82	3.22
SD	0.20	0.15	0.24	0.21	0.17	0.18	0.19	0.14	0.19	0.17
C.V.	3.85	8.20	5.26	8.50	4.42	5.88	4.73	4.12	3.94	5.28
Skewness	—	—	−.49	−.52	1.29	0.01	0.27	−.54	0.76	0.50
Diacodexis gracilis										
Range			3.9–4.0	2.2–2.3	3.7–3.8	2.8	3.7–3.9	3.3–3.8	4.5–4.8	3.00
N			2	2	3	3	3	3	2	2
Mean			3.95	2.25	3.77	2.80	3.83	3.47	4.65	3.00
SD			—	—	0.06	—	0.12	0.29	—	—
C.V.			—	—	1.59	—	3.13	8.36	—	—
Artiodactyla sp. A.										
Range		1.50	4.1–4.9	2.1–2.3	3.7–4.2	2.7–2.9	4.0–4.3	3.2–3.6	4.7–5.2	2.8–3.3
N		1	3	3	2	5	7	8	9	9
Mean		1.50	4.50	2.17	3.95	2.80	4.14	3.39	4.97	3.09
SD		—	0.40	0.12	—	0.07	0.11	0.12	0.18	0.15
C.V.		—	8.89	5.53	—	2.50	2.66	3.54	3.62	4.85
Skewness		—	—	—	—	0.00	−.18	0.24	−.02	−.68

Table 2.—*Summary statistics of upper dentitions of* Diacodexis secans *(lineage segments* Diacodexis secans-primus, D. secans-metsiacus, D. secans-kelleyi, D. secans-secans*),* D. minutus, D. gracilis, *and Artiodactyl sp. A.*

Taxa and statistics	P^3		P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W	L	W
Diacodexis secans-secans										
Range	5.6–6.0	3.7–4.0	4.0–4.3	4.7–5.8	4.0–4.8	5.3–6.9	4.5–5.5	5.9–7.3	4.4–5.0	6.0–7.0
N	2	2	6	7	19	19	26	26	17	18
Mean	5.80	3.85	4.13	5.14	5.70	4.37	4.88	6.59	4.71	6.44
SD	—	—	0.14	0.37	0.18	0.25	0.29	0.38	0.22	0.38
C.V.	—	—	3.39	7.20	4.12	4.39	5.94	5.77	4.67	5.90
Skewness	—	—	0.38	0.59	−.63	0.16	0.21	−.16	0.11	0.77
Diacodexis secans-kelleyi										
Range	5.00	5.20	3.6–4.5	4.3–5.1	3.8–4.6	4.8–5.6	3.8–4.7	5.6–6.4	3.9–4.3	5.4–6.3
N	1	1	5	6	11	12	34	34	17	16
Mean	5.00	5.20	3.88	4.67	4.25	5.30	4.42	6.03	4.11	5.93
SD	—	—	0.38	0.27	0.25	0.23	0.22	0.21	0.16	0.23
C.V.	—	—	9.80	5.78	5.88	4.34	4.98	3.48	3.89	3.87
Skewness	—	—	0.94	0.32	−.23	−.80	−.56	−.05	−.20	−.56
Diacodexis secans-metsiacus										
Range		3.30	3.4–4.1	4.4–5.1	3.9–4.4	5.0–5.5	4.1–4.7	4.8–6.3	3.7–4.5	5.1–6.3
N		1	6	6	6	6	7	7	6	6
Mean		3.30	3.82	4.75	4.15	5.20	4.41	5.77	4.12	5.72
SD		—	0.26	0.27	0.23	0.19	0.23	0.51	0.31	0.40
C.V.		—	6.81	5.68	5.54	3.65	5.22	8.84	7.52	6.99
Skewness		—	−.34	0.00	0.00	0.38	−.10	−.85	−.03	−.11

Table 2.—*Continued.*

Taxa and statistics	P^3		P^4		M^1		M^2		M^3	
	L	W	L	W	L	W	L	W	L	W
Diacodexis secans-primus										
Range	5.1–5.6	3.70	3.4–4.0	4.4–5.0	3.7–4.2	4.6–5.4	4.0–4.7	4.9–6.2	3.5–4.6	5.0–6.0
N	2	1	5	5	18	16	15	16	13	13
Mean	5.45	3.70	3.70	4.64	3.94	5.01	4.33	5.68	4.14	5.59
SD	—	—	0.24	0.33	0.15	0.23	0.21	0.30	0.32	0.35
C.V.	—	—	6.49	7.11	3.81	4.59	4.85	5.28	7.73	6.26
Skewness	—	—	0.00	0.69	−.48	0.23	−.07	−.83	−.29	−.32
Diacodexis minutus										
Range	4.60	3.10			3.2–3.7	4.5–5.2	3.6–4.0	5.0–5.9		
N	1	1			5	5	6	8		
Mean	4.60	3.10			3.52	4.82	3.85	5.26		
SD	—	—			0.20	0.28	0.16	0.31		
C.V.	—	—			5.71	5.81	4.16	5.89		
Skewness	—	—			−.69	0.32	−.59	1.20		
Diacodexis gracilis										
UCM 52585	4.80	2.50	3.60	4.00	3.60	4.20	3.90	4.80	3.50	4.40
Artiodactyl sp. A										
Range					3.6–3.9	4.4–5.0	3.7–4.5	5.4–6.0	3.4–4.1	5.5–6.3
N					3	3	4	4	2	2
Mean					3.73	4.73	4.13	5.68	3.75	5.90
SD					0.15	0.31	0.33	0.25	—	—
C.V.					4.02	6.55	7.99	4.40	—	—

Table 3.—*Dimensions of lower teeth of* Diacodexis secans, *lineage segment* D. s.-secans.

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 22503	CM 34	6.3	2.0			4.6	3.8	4.9	4.4	6.4	4.6
CM 22503	CM 34			6.1	3.3	4.5	3.7				
CM 42125	CM 34	6.2	2.2	5.6	3.0						
CM 55151	CM 34	6.0	2.3								
CM 42097	CM 1084	6.4	2.3								
UCM 42199	CM 34	7.0	2.4	5.8	3.1	4.4	3.4	4.6	4.3	6.7	4.2
CM 55133	CM 34	7.3	2.7								
CM 21213	CM 99			5.2	3.3	4.3	3.9	4.3	4.5		4.7
CM 37300	CM 34			5.6	3.4			4.8	4.4	6.4	4.4
CM 55164	CM 34			5.7	2.8	4.4	3.6				
CM 22532	CM 34			5.3	2.9						
CM 40770	CM 34			5.7	2.9	4.7	3.5				
CM 40779	CM 34			5.6	2.5						
CM 22511	CM 90			5.4	2.7	4.3	3.2	4.5	3.9		
CM 30947	CM 34			5.6	2.9	4.3	3.4	4.6		6.0	4.0
CM 21228	CM 34			5.5	3.4	4.6	3.4				
CM 55362	CM 34			5.7	3.0	4.3	3.5				
AMNH 4899*	WRB			5.5	2.7	4.7	3.5	4.8	4.0	6.5	4.0
AMNH 4899*	WRB			5.7	2.8	4.5	3.5	4.8	4.0	6.3	4.0
AMNH 14937**	CM 34			5.7	3.2	4.7	4.1	5.0	5.0		4.8
PU 20598	CM 34			5.3	3.0	4.6	3.7				
PU 20599	CM 34			5.3	2.6	4.5	3.3				
PU 20599	CM 34					4.5	3.6	4.7	4.1	6.8	4.5
PU 20800	Alkali Cr			6.2	3.4	4.8	3.8				
CM 43735	CM 1040			5.8	3.0	4.5	4.0				
CM 35732	CM 34					5.0	3.5	5.0	4.1	6.2	4.0
CM 43479	CM 1077					4.8	3.7				
CM 30951	CM 34						3.7		4.4		
CM 44911	CM 216					4.6	3.7				
UCM 46508	UCM 79041					4.3	3.5				

Table 3.—*Continued.*

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 55156	CM 34					4.9		5.2	4.6		
CM 55141	CM 34						3.5	4.5	4.3	6.8	4.3
CM 55366	CM 34					4.5	3.8	5.0	4.5		
CM 30951	CM 34						3.7	4.7	4.5		
CM 55353	CM 34					4.4	3.8				
CM 21020	CM 34					4.9	3.4	4.5	4.4		
CM 21140	CM 34					4.6		4.8	4.3	6.8	4.3
CM 22504	CM 34					4.0	3.4	4.4	4.0		
CM 22506	CM 34					4.5	3.9	4.9	4.7		
CM 35777	CM 34					4.5	3.5	4.6	4.5	6.3	4.3
CM 55368	CM 34					4.4	3.9		4.4		4.4
CM 55357	CM 34					4.6	3.8	5.0	4.5		
CM 55167	CM 34					4.4	3.6	5.0	4.5	6.7	4.9
CM 42087	CM 1040					4.4	4.0	4.5	4.8		
CM 30944	CM 34					4.5	3.7				
CM 42082	CM 1039					4.4	3.6	4.8	4.5	6.3	4.7
CM 42082	CM 1039					4.3	3.5	4.6	4.4	6.1	4.6
PU 22317	CM 34					5.1	3.9	5.2	4.5		
PU 22317	CM 34						4.0				
PU 22471	Alkali Cr					4.5	3.3				
CM 35776	CM 34							4.8	4.3	6.8	4.2
CM 21017	CM 34							5.3	5.0	7.0	4.8
CM 21135	CM 34							4.9	4.4	6.0	4.4
CM 21136	CM 34							4.4	4.4	6.0	4.2
CM 21137	CM 34							4.7	4.4	5.4	
CM 21138	CM 34							5.2	4.6	6.3	4.2
CM 22508	CM 34							4.8	4.3	6.1	4.4
CM 35771	CM 34							4.7	4.2	6.0	4.5
CM 30948	CM 34							4.7	4.4	6.7	4.3

Table 3.—*Continued.*

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 55158	CM 34							4.6	4.4	6.1	4.4
CM 55140	CM 34							4.7	4.3		
CM 40780	CM 34							4.9	4.5		
CM 40764	CM 34							4.8	4.4	6.0	4.2
CM 40764	CM 34									6.3	4.3
CM 40781	CM 34							5.0	4.5		
CM 30945	CM 34								4.2	6.6	4.2
CM 30950	CM 34							4.8		5.7	4.8
CM 36441	CM 34							5.1	4.6		
CM 37308	CM 34							4.4	3.9		
CM 30946	CM 34							4.3	3.9	5.8	4.1
CM 55160	CM 34							5.0	4.6		
CM 27480	CM 34							4.7	4.3		
CM 30891	CM 34							4.6	4.2		
CM 36931	CM 34							4.6	4.3	6.6	4.3
CM 36934	CM 34							5.3	4.3	6.6	4.2
CM 43711	CM 34							5.0	4.5		
CM 43736	CM 91							5.3	5.3	7.0	4.9
CM 44846	CM 1534							4.5	4.4	6.3	4.3
CM 44849	CM 1040							4.9	4.8	6.4	4.5
AMNH 4202***	BHB									6.3	4.5
UCM 47026	UCM 81008									7.1	4.4
CM 44909	CM 34									6.2	4.3
CM 43469	CM 34									6.3	4.5
CM 55360	CM 34									6.8	4.5
CM 40784	CM 34									6.5	4.0
CM 36444	CM 34									6.3	4.5

Table 3.—*Continued.*

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 36445	CM 34										4.6
CM 35772	CM 34									6.6	4.4
CM 35774	CM 34									6.1	4.2
CM 35775	CM 34									6.4	4.1
CM 55359	CM 34										4.1
CM 55168	CM 34										4.0
CM 55169	CM 34									6.1	4.0
CM 42096	CM 34									6.4	4.7
CM 40776	CM 34									5.6	3.7
Mean		6.53	2.32	5.62	3.00	4.53	3.64	4.79	4.41	6.36	4.35
N		6	6	20	20	39	41	53	54	47	52

* Holotype of *Diacodexis secans*.
** Holotype of *Diacodexis olseni*.
*** Holotype of *Diacodexis laticuneus*.

Table 4.—*Dimensions of upper teeth of* Diacodexis secans, *lineage segment* D. s.-secans.

Specimen no.	Locality	P^3		P^4		M^1		M^2		M^3	
		L	W	L	W	L	W	L	W	L	W
CM 21217	CM 99	5.6	4.0								
CM 43476	CM 1040	6.0	3.7	4.1	5.8	4.0	5.9	4.7	6.5	5.0	7.0
CM 55162	CM 34			4.3	5.4						
CM 55351	CM 34			4.0	4.7	4.1	5.3				
CM 35780	CM 34			4.3	4.8	4.5	5.6	4.8	6.0		
CM 22507	CM 34			4.0	5.2	4.6	5.8	5.0	6.6		
CM 42082	CM 1039			4.1	5.1	4.2	5.5	4.8	6.6	4.6	6.7
CM 43717	CM 34				5.0	4.1	5.5	4.6	6.0		
CM 27455	CM 34					4.4	5.3	4.5	5.9		
CM 44908	CM 34					4.6	6.2	5.0	6.9	4.8	6.8
CM 43477	CM 1077							4.8	6.9	4.6	6.5
CM 51636	CM 1096					4.2	6.0				
UCM 44906	CM 34					4.3	5.9				
UCM 46809	UCM 80062					4.4	6.0				
UCM 46811	UCM 80062					4.4	5.9				
CM 42080	CM 1038					4.4	5.5				
CM 21104	CM 34					4.4	5.6				
CM 35782	CM 34					4.5	5.7				
CM 42073	CM 34					4.5	5.5				
CM 42079	CM 1036					4.5	5.6				
CM 40778	CM 34					4.5	5.8			4.5	6.2
CM 37299	CM 34							5.1	6.6		
CM 22532	CM 34							4.7	6.3		
CM 35778	CM 34							5.1	6.8		
CM 37304	CM 34							4.5	6.2		
CM 55166	CM 34							4.5	6.8		
CM 35783	CM 34							5.0	6.6		
CM 55356	CM 34							5.0	7.0		
CM 42074	CM 34							4.8	6.5		

Table 4.—*Continued.*

		P^3		P^4		M^1		M^2		M^3	
Specimen no.	Locality	L	W	L	W	L	W	L	W	L	W
CM 21063	CM 34							5.4	7.0		
CM 43730	CM 1040							5.0	6.8		
CM 43731	CM 1040							5.1	6.7		
CM 43732	CM 1040							5.5	7.0		
CM 37307	CM 34							4.6	6.0		
CM 43475	CM 1040							5.3	7.3	5.0	7.2
CM 43734	CM 1040							5.2	7.2	4.9	7.2
CM 43744	CM 34							4.4	6.3	4.5	6.2
CM 44909	CM 34							5.0	6.6	4.8	6.5
CM 55358	CM 34							4.5	6.3	4.4	6.0
CM 35784	CM 34									4.4	6.3
CM 55165	CM 34									4.5	6.1
CM 21025	CM 34									4.7	6.2
CM 22509	CM 92									4.5	6.0
CM 22510	CM 90									4.7	6.4
CM 36439	CM 92									5.0	6.0
CM 37302	CM 34									4.8	6.4
CM 43737	UCM 81010										6.2
UCM 44341	UCM 80062									5.0	6.5
Mean				4.13	5.14	4.37	5.70	4.88	6.59	4.71	6.44
N				6	7	18	18	26	26	18	19

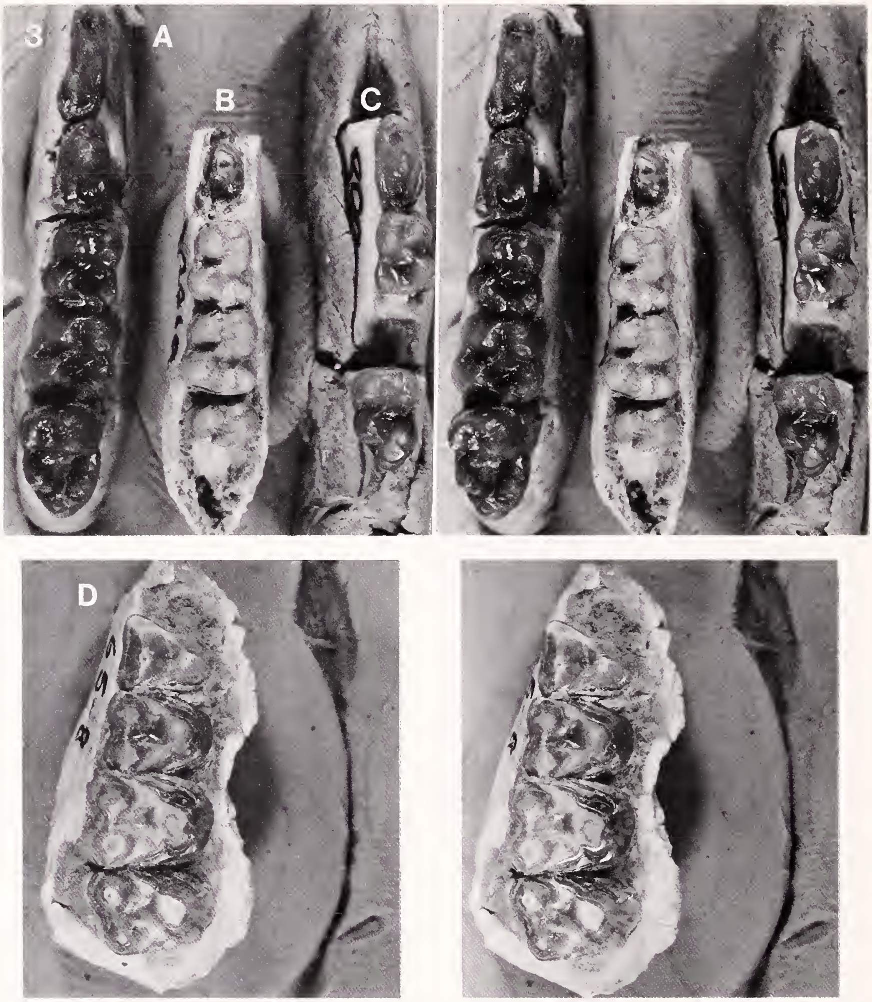


Fig. 3.—*Diacodexis secans* (lineage segment *D. s.-kelleyi*). (A) CM 39880; (B) CM 22810; (C) CM 39221; (D) CM 22803; all approx. ×2.

associated upper molars in AMNH 4202 are *Hyopsodus powellianus* (including *H. walcottianus*), a Lysitean-Lostcabinian species.

Lineage Segment *Diacodexis secans-kelleyi*
(Fig. 3; Tables 1–2, 5–6)

Etymology.—In honor of Dana R. Kelley for his contributions to the paleontology of the Lysite Member, Wind River Formation.

Diagnosis.—Intermediate in mean size and robusticity of all teeth between lineage segments *D. s.-metsiacus* and *D. s.-secans*. Frequency and degree of expression of the following features higher compared to *D. s.-primus* and *D. s.-metsiacus* and lower compared to *D. s.-secans*: inflation of molar protocones, metaconids, and hypoconids; development of molar postmetacristids and talonid notches; elongation of $P^3/_3$, P_4; shortness of M_3 talonid. Unlike *D. s.-primus*, P^3 protocone stronger, with metacone (when present) closer to paracone, and lower molars with slightly more medial paraconid.

Diagnostic series.—CM 20872, 22801, 22803, 22809–22811, 35932, 37104, 39875, 39880, 39921, 44906; AMNH 4691 ("paratype" of *D. chacensis*); ACM 2405, 2408, 2411, 2674; PU 22540, 22546; UCM 40463.

Referred specimens.—CM 19864, 19866, 20872, 20910, 22801–22817, 28688, 28689, 28908, 28924, 28938, 29177, 35930, 35932, 36062, 36063, 36534, 37101–37109, 39218–39220, 39246–39248, 39283, 39469, 39625, 39648, 39649, 39768, 39769, 39871–39880, 39895, 39896, 39906, 39920–39924, 39968, 42095, 42101–42105, 42107–42113, 43708, 43721, 44906, 44912, 53791, 53793, 54124–54126, 54160, 54161, 54212, 54213; AMNH 4691 ("paratype" of *D. chacensis*), 56565; ACM 2403, 2405, 2406, 2408–2414, 2417, 2418, 2512, 2603–2609, 2624, 2671, 2674, 2676, 2680, 2707, 2708, 2738, 2751, 2900, 2901, 2940, 3425, 3475, 3528, 4320, 4324, 4374, 4375, 11070, 11084, 11133, 11134, 11165, 11224, 11251, 11252, 11254; PU 17697, 22540–22542, 22546, 22771, 22772; UCM 40463.

Localities.—CM locs. 112, 118, 793, 797, 799, 800, 801, 802, 805, 807, 927, 928, 931, 1007, 1008; ACM locs. 03-425, 03-476, 03-528, 51-L9, 51-L10, 51-L15, 51-L19, 51-L29, 51-L34, 57-28, 57-30, 57-31, 60-112, 60-118, 61-01, 61-02, 62-06, 62-10, 62-11, 62-15, 62-16, 62-17, 62-33, 62-34, 62-35, 62-38, 63-04, 63-06, 63-11, 63-20, 63-28; UCM Loc. 78186 (all Lysitean, Lysite Mbr., Wind River Fm.). CM loc. 1049 (Lysitean or Lostcabinian, Lost Cabin Mbr., Wind River Fm.); AMNH Locs. "*Coryphodon* beds" (Willwood Fm., Bighorn Basin), Huerfano Loc. 8 (Huerfano Fm., Huerfano Basin).

Known distribution.—Lysitean to ?Lostcabinian—Wind River Basin (Wind River Fm.), Wyoming; Lysitean—Huerfano Basin (Huerfano Fm.), Colorado. ?Lysitean—Bighorn Basin (Willwood Fm.), Wyoming.

Discussion.—*D. s.-kelleyi* overlaps significantly at either end of its range of variation with both the temporally younger *D. s.-secans* and older *D. s.-metsiacus* in size and morphology. Mean values and frequencies of $P^3/_3$ and $P^4/_4$ length, inflation of molar protocones, metaconids and hypoconids, and development of the postmetacristid and talonid notch on M_{1-3} for *D. s.-kelleyi* are intermediate between those in *D. s.-metsiacus* and *D. s.-secans*. These features, as well as paraconid strength and talonid width on M_2, show continuous, normally distributed variation in *D. s.-kelleyi*. The protocone on P^3 occurs either di-

Table 5.—*Dimensions of lower teeth of* Diacodexis secans, *lineage segment* D. s.-kelleyi.

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
ACM 2626	ACM 62-11	5.4	1.6								
CM 22817	CM 807	5.6	1.6		2.4						
CM 39625	CM 802			5.3	2.8						
CM 39768	CM 805			4.9	3.2						
CM 39876	CM 797			4.6	2.5						
CM 39896	CM 807			5.3	2.8						
CM 42107	CM 797			4.9	2.3						
CM 54126	CM 807			4.9	2.5						
CM 53793	CM 807			4.8	2.7						
CM 42105	CM 800			4.7	2.6						
CM 42109	CM 797			5.2	2.6	4.2	3.8				
CM 19864	CM 807			4.8	2.5	4.3	3.0				
CM 20910	CM 807			5.0	2.9	4.5	3.6				
CM 29177	CM 807			5.0	2.7	4.2	3.1				
CM 36534	CM 807			5.3	2.6	4.3	3.3				
CM 39247	CM 793			4.4	2.7	4.5	3.2				
CM 42104	CM 797			4.4	2.4	4.5	3.2				
CM 22812	CM 928			4.7	2.8	4.2					
CM 22801	CM 931			4.7	2.6	4.3	3.5				
ACM 3528	ACM 03-528			4.9	3.0						
ACM 3528	ACM 03-528			4.7	2.8	4.3	3.3				
CM 39906	CM 927			4.7	2.7			4.7	3.7		
PU 22771	CM 797			4.7	2.6	4.3	3.6	4.8	4.4		
CM 39872	CM 797			4.5	2.8	4.0	3.3	4.4	4.0		
CM 22805	CM 801			4.7	2.5	4.2	3.3	4.5	3.8		
PU 22542	CM 799			5.3	2.8	4.2	3.4	4.2	4.1		
PU 22542	CM 799					4.0	3.5	4.3	4.0		
PU 22546	CM 799			5.1	2.4	4.1	3.1	4.4	3.6		3.6
AMNH 4691*	Coryphodon beds			4.7	2.5	4.6	3.5	4.8	4.1	5.9	4.0

Table 5.—*Continued.*

Specimen no.	Locality	P_3 L	P_3 W	P_4 L	P_4 W	M_1 L	M_1 W	M_2 L	M_2 W	M_3 L	M_3 W
CM 42103	CM 802			4.2	2.5	4.1	3.3	4.4	3.7		
CM 43708	CM 1049			4.6	2.1					5.4	3.4
CM 39921	CM 800			4.7	2.5					5.0	3.3
CM 39921	CM 800			4.5	2.4	4.2	3.4				
CM 39880	CM 800			4.9	2.9	4.3	3.6	4.5	4.4	6.0	3.1
CM 22809	CM 118			4.8	2.6				3.8	5.8	3.7
ACM 2403	ACM 62-38			5.2	2.5	4.1	3.1	4.2	3.9		
CM 22810	CM 118			4.2	2.3	4.0	3.0	4.2	3.7		3.5
CM 22810	CM 118					4.3	3.1	4.2	3.8	6.0	4.1
CM 20872	CM 807				2.6	4.3	3.4	4.4	3.8	6.0	4.1
CM 37104	CM 799					4.6	3.6	4.8	4.3	6.0	3.6
AMNH 56565	Huerfano 8					4.5	3.0				
CM 44906	CM 799					4.1	2.8				
CM 54212	CM 799					4.1	3.2				
CM 54213	CM 799					4.1	3.2	4.7	3.6		3.5
CM 22811	CM 928					4.3	3.0	4.3			
CM 42112	CM 797					4.5	3.5	4.5	4.0		
CM 42108	CM 797					4.5	3.4	4.7	4.2		
CM 54125	CM 807					4.0	3.2	4.6	3.7		
CM 42095	CM 1008					4.2	3.2				
CM 37106	CM 807					4.1	3.5	4.5	3.6	5.4	3.4
CM 28924	CM 807					4.2	3.4	4.5	4.3		
CM 19866	CM 807					4.1	3.2	4.2			
CM 37106	CM 807					4.1	3.2	4.5	3.6	5.6	
CM 39873	CM 797					4.1	3.2	4.3	3.8	5.7	3.5
CM 39920	CM 800					4.3	3.0	4.5	4.0		
CM 22802	CM 799					4.0		4.0	3.8		
CM 39871	CM 797					4.2	3.3	4.4			
CM 36062	CM 799					4.3	3.3	4.6	4.0	6.0	3.7

Table 5.—*Continued.*

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 22807	CM 799					4.5	3.6				
CM 42102	CM 800					4.4	3.6				
PU 22772	CM 799					4.2	3.2				
ACM 2512	ACM 62-35					4.4	3.4	4.4	3.9		
ACM 2900	ACM 61-01					4.2	3.5				
ACM 2410	ACM 62-16					4.2	3.6				
ACM 2680	ACM 61-01							4.7	4.2		
ACM 4324	ACM 63-11							4.3	4.0		
ACM 2607	ACM 57-30							4.3	3.5		
ACM 2624	ACM 57-31							4.5	4.1		
CM 39879	CM 929							4.9	3.8		
CM 39218	CM 931							4.7	4.0		
CM 39922	CM 800							4.6			
CM 28908	CM 797							4.6	4.2		
CM 37105	CM 931							4.9	4.5		
CM 39469	CM 112							4.8	4.1		
CM 22814	CM 807							4.5	3.9	5.5	3.7
CM 22814	CM 807							4.5	4.2		
CM 39283	CM 112							4.8	4.3	5.8	4.0
CM 42113	CM 797							4.7	4.0	5.5	3.6
CM 37101	CM 807							4.0	4.2	5.6	3.8
CM 37102	CM 807							4.3	4.1	6.0	3.7
CM 39874	CM 797							4.5	4.0	5.7	4.1
CM 39875	CM 797							4.8	4.5	6.0	4.5
CM 39968	CM 928							4.3	4.0	5.6	4.0
CM 22806	CM 799							4.5	3.5	5.9	
UCM 40463	CM 797								3.7	5.6	3.5
PU 17697	CM 799							4.7	4.2	6.0	4.0
ACM 11251	ACM 51-L34							4.2	3.5	5.6	3.4
ACM 11252	ACM 51-L34							4.2	4.2	5.7	4.0

Table 5.—*Continued.*

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
ACM 3425	ACM 03-425							4.7	4.1		3.5
ACM 2405	ACM 62-06							4.2	4.2	5.6	3.4
ACM 2708	ACM 60-118							4.2	4.0	5.1	3.6
ACM 2408	ACM 62-15							4.2	3.7	5.6	3.7
ACM 2751	ACM 60-118							4.2	4.1		
CM 22813	CM 799									5.7	4.0
CM 22816	CM 807									5.6	3.5
CM 36063	CM 799									6.0	4.0
CM 37103	CM 807									5.5	3.4
CM 37108	CM 797									5.6	3.9
CM 37109	CM 807									5.6	3.6
CM 39769	CM 805									6.0	4.0
CM 39877	CM 797									6.0	3.8
CM 39923	CM 800									6.1	3.7
CM 42101	CM 799									6.1	3.9
PU 22541	CM 799									5.6	3.4
ACM 2608	ACM 57-28									5.2	3.7
ACM 2409	ACM 62-33									5.3	3.7
ACM 2406	ACM 62-34									5.5	3.8
ACM 11133	ACM 51-L15									6.3	4.0
ACM 11134	ACM 51-L15									5.5	3.5
ACM 11165	ACM 51-L19									5.7	3.8
ACM 11254	ACM 51-L34									6.2	3.8
ACM 3475	ACM 03-476									5.5	3.7
ACM 4375	ACM 63-04									5.9	3.8
ACM 4375	ACM 63-04									6.4	3.8
CM 44912	CM 1007									5.6	3.6
Mean				4.80	2.61	4.25	3.31	4.47	3.97	5.73	3.72
N				34	36	49	47	58	56	50	52

* "Paratype" of *Diacodexis chacensis* (Cope, 1884).

rectly lingual to the paracone (CM 35932) as in *D. s.-metsiacus* and *D. s.-primus* or slightly more posteriorly (ACM 2674), but not as posteriorly as in *D. s.-secans.* Presence of a P^3 metacone is variable. Both the postmetacristid and talonid notch on M_{1-3} occur more frequently than in *D. s.-metsiacus,* but are weakly developed, even on the robust specimens that overlap in size and degree of cusp inflation with *D. s.-secans.* Compared to the latter, the protocone on M^{1-3} of *D. s.-kelleyi* is less bulbous, resulting in a more distinct postprotocrista, pseudohypocone, cingular hypocone, and pericone, and more complete isolation of the metaconule from the postprotocrista. The cingular hypocone and pericone are better and more frequently developed than in *D. s.-primus* and *D. s.-metsiacus.* On ACM 2417, the extreme development of the pericone distends the anterolingual base of the crown. Some of the upper molars, especially M^3, have an incipient mesostyle at the base of the centrocrista, as well as slight swelling on the ectocingulum labial to the centrocrista.

CM 39921, 54212 and 44906 are the smallest and most gracile in the *D. s.-kelleyi* sample, whereas CM 39880, 39874, 39875, and 28924 are the largest and most robust. These specimens show the greatest degree of overlap with *D. s.-metsiacus* and *D. s.-secans,* respectively. Isolated P_4s and M_1s of *D. s.-kelleyi* exhibit to a much lesser degree the morphological differences (cusp inflation, larger size) between this lineage segment and *D. s.-metsiacus* than do M_2s and M_3s.

On CM 37104 the cristid obliqua on M_1 extends weakly to the metaconid in a manner somewhat reminiscent of *Antiacodon*; this feature occurs much more frequently on M_1s of *D. s.-metsiacus.* However, the molars on CM 37104 as well as those of both lineage segments differ from those of *Antiacodon* in being more bulbous (inflated hypoconid, metaconid, and paraconid), and in having a much shallower talonid and trigonid basin, a smaller hypoconulid, a weaker cristid obliqua that is not directed toward the metaconid on M_{2-3}, and a lower, less compressed trigonid. Similarly, CM 22810 resembles *Hexacodus uintensis* in size and position of the molar cusps, but lacks many of the derived features of the latter—the strong hypocristid directed toward the entoconid, the broad postcingulid, the high and conical entoconid, the severely reduced paraconid, and the elevated paraconid and metaconid.

The three small specimens of *D. s.-kelleyi* listed above also approach *D. minutus* in size and morphology except for the slight metaconid inflation on M_1 and the weaker postmetacristid and talonid notch on M_1 and M_3. These specimens may well represent the most primitive expression of *D. minutus,* but referral to the latter is unwarranted at this point, given that they preserve only P_4, M_1, and M_3, which are less diagnostic than M_2. The M_3 in CM 39921 is indistinguishable from

M_3s of Gardnerbuttean *D. minutus*, yet this and other small specimens fall within the lower part of the range of variation of *D. s.-kelleyi.* Importantly, the entire range of morphological variation (normally distributed) of *D. s.-kelleyi* includes the incipient and/or moderate development of features ($P^3/_3$ elongation; molar postmetacristid, talonid notch, metaconid inflation, paraconid reduction; squareness of M_{1-2}) that appear to be canalized and amplified (in frequency and degree of expression) in temporally younger *D. s.-secans, D. woltonensis,* and *D. minutus.*

Lineage Segment *Diacodexis secans-metsiacus*
(Fig. 4; Tables 1–2, 7–8)

Diagnosis.—Smaller (mean size) and less robust than lineage segment *D. s.-kelleyi* and *D. s.-secans,* with P_2 and $P^3/_3$ shorter, P^3 protocone smaller, P_3 shorter than M_3, molars less bunodont, M_{1-2} less nearly square, less inflated molar protocones, conules, protoconids, metaconids, hypoconids and more distinct protocristae, conulecristae and pseudohypocones; M_{1-3} postmetacristid often absent or extremely weak, talonid notch weak; slightly smaller (mean size) than lineage segment *D. s.-primus* with P_3 usually longer, P_4 postmetacristid present, P_4 paraconid usually double, molar paraconids slightly medial relative to metaconid, talonid notch present, shorter M_3 hypoconulid lobe, P^3 metacone stronger and closer to the paracone.

Diagnostic series.—CM 12419; AMNH 4696 (cotype of *D. metsiacus*), 4700 (holotype of *D. brachystomus*), 15522, 15666; UCM 19427, 52551–52553; USGS 2352.

Referred specimens.—CM 12368, 12395, 12396, 12419, 53912, 58131, 58132, 58134, 58137; AMNH 4696 (cotype of *D. metsiacus*), 4700 (holotype of *D. brachystomus*), 15522, 15666; UCM 19427, 44125–44128, 44131, 45778, 45783, 47604, 52551–52578, 52586–52598; USGS 2352.

Localities.—CM locs. 147, 673, 843; UCM locs. 80024, 80066, 81092, 84168, 84172, 84177, 84178, 84180, 84181, 84183, 84248, 84249, 84254, 84255, 85227, 85237, 85257, 85258; AMNH locs. *Coryphodon* beds, St. Joe, Dorsey Creek; (all late Graybullian, Willwood Fm.), Bighorn Basin, Wyoming.

Known distribution.—Early Wasatchian (late Graybullian)—Bighorn Basin (Willwood Fm.), Wyoming.

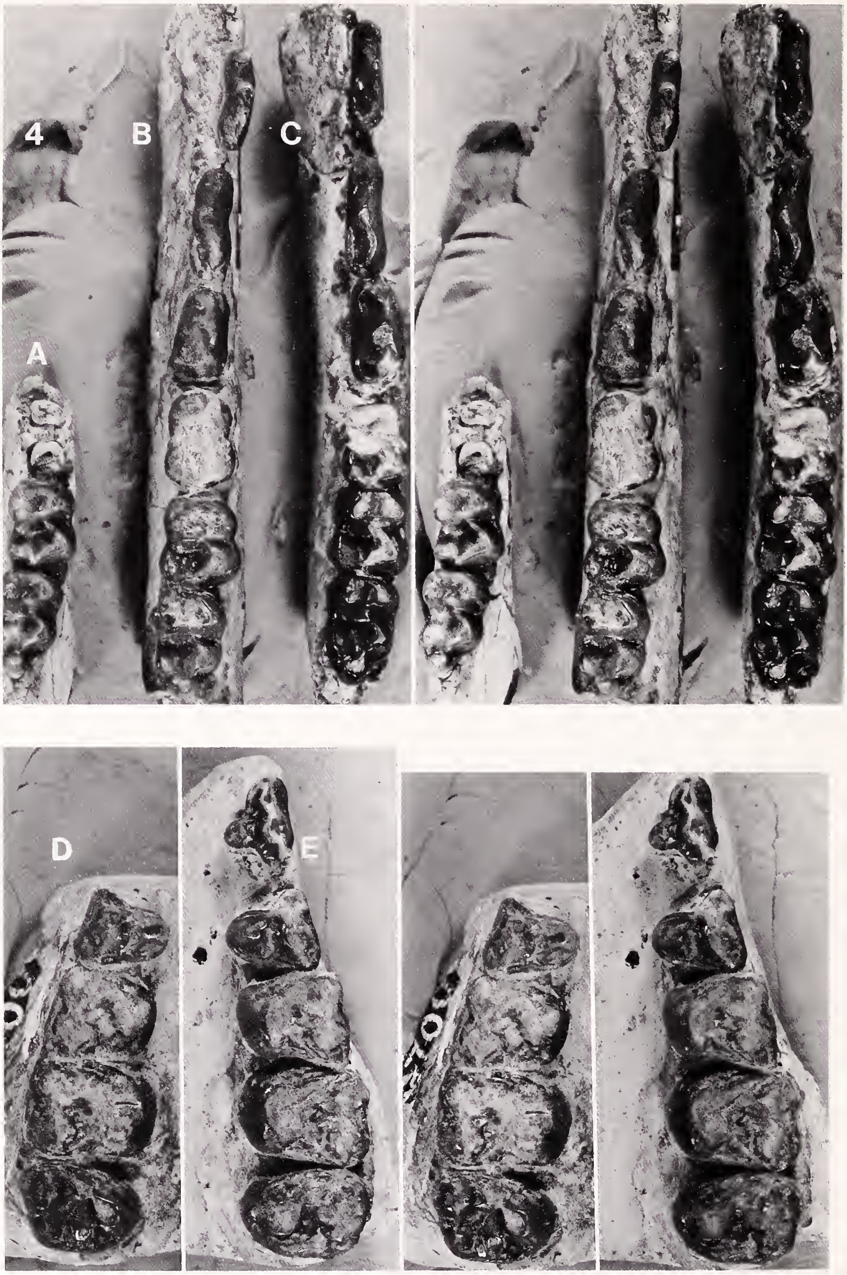
Discussion.—The material referred to the lineage segment *D. s.-metsiacus* includes the holotype of *D. brachystomus* and the cotype of *D. metsiacus.* These specimens are at the opposite ends of the range of variation of normally distributed and penecontemporaneous samples from the *Bunophorus* interval zone of the Willwood Formation (late Graybullian). Features that distinguish these two specimens are con-

Table 6.—*Dimensions of upper teeth of* Diacodexis secans, *lineage segment* D. s.-kelleyi.

		P^3		P^4		M^1		M^2		M^3	
Specimen no.	Locality	L	W	L	W	L	W	L	W	L	W
ACM 2674	ACM 60-115	5.0	5.2								
CM 43721	CM 797			3.6	4.5						
ACM 2411	ACM 62-36				4.3	3.8	4.8	3.8	5.6	3.9	5.4
CM 22802	CM 799			4.5	5.1	4.5	5.5	4.4	6.2	4.2	6.0
CM 22803	CM 799			3.6	4.6	4.1	5.2	4.4	6.0	4.1	6.0
CM 22808	CM 807			4.0	4.7	4.6	5.5	4.4	5.9	4.2	5.8
CM 35932	CM 929			3.7	4.8	4.4	5.6	4.4	6.4		
CM 28688	CM 807					4.0	5.3	4.5	6.3	4.2	6.0
CM 54124	CM 807					4.2	5.3	4.3	5.9	4.0	6.0
PU 22540	CM 799					4.4	5.4	4.7	6.0		
CM 53791	CM 807						5.3				
ACM 2603	ACM 57-30					4.0	5.0				
ACM 2606	ACM 57-30					4.2	5.2				
ACM 4375	ACM 63-04					4.5	5.5				
ACM 2417	ACM 62-38							4.1	6.0	3.9	5.6
CM 39246	CM 793							4.1	5.6	3.9	5.9
CM 22815	CM 807							4.4	6.0	4.3	5.7
CM 39649	CM 802							4.3		3.9	
CM 42111	CM 797							4.3	6.1		
CM 35930	CM 929							4.4	6.2		
CM 28938	CM 797							4.5	6.3		
CM 39648	CM 802							4.3	6.0		
CM 39248	CM 793							4.5	6.0		
CM 37107	CM 931							4.2	6.0		
CM 39219	CM 931								6.0		

Table 6.—*Continued.*

Specimen no.	Locality	P³		P⁴		M¹		M²		M³	
		L	W	L	W	L	W	L	W	L	W
CM 54160	CM 807							4.7	6.4		
CM 39220	CM 931							4.6	6.0		
CM 54161	CM 807							4.5	6.0		
CM 39924	CM 800							4.4	5.9		
CM 39924	CM 800							4.3	5.8		
CM 39906	CM 927							4.5	6.0		
CM 39906	CM 927							4.5	6.2		
ACM 2604	ACM 57-30							4.4	6.0		
ACM 2605	ACM 57-31							4.5	5.9		
ACM 2609	ACM 57-31							4.6	5.8		
ACM 2412	ACM 62-17							4.4	6.0		
ACM 2413	ACM 62-10							4.0	5.7		
ACM 2414	ACM 62-11							4.7	6.3		
ACM 2901	ACM 61-02							4.7	6.3		
ACM 2940	ACM 61-02							4.5	5.8		
ACM 11084	ACM 51-L10							4.5	6.3		
ACM 2418	ACM 62-38									4.3	6.0
ACM 4375	ACM 63-04									4.3	6.2
ACM 11070	ACM 51-L9									4.0	5.9
CM 28689	CM 807									4.2	6.2
CM 28689	CM 807									4.2	6.3
CM 42110	CM 797									4.0	5.8
CM 39878	CM 797									4.3	6.0
Mean				3.88	4.67	4.25	5.30	4.41	6.03	4.11	5.93
N				5	6	11	12	34	34	17	16


4
B
C
A
D
E

tinuously variable among these samples and include size, trigonid elevation, and degree of molar (especially metaconid) inflation.

The holotype of *D. brachystomus* and the other larger specimens in *D. s.-metsiacus* overlap morphologically with material in the lower part of the range of variation of *D. s.-kelleyi* and with *D. s.-primus* in size, whereas the cotype of *D. metsiacus* is remarkably similar to some of the late Graybullian and/or early Lysitean material from the San Juan and Piceance basins assigned to Artiodactyla sp. A (see below). Resemblances here include small size and an elevated paraconid-metaconid wall on M_{1-3}, one of the major derived features of Artiodactyla sp. A. The latter is further derived in having higher trigonids, broad postcingulids, and strong, isolated hypoconulids close to tall entoconids on the molars. As in *D. s.-metsiacus,* the molar metaconids on the cotype of *D. metsiacus* are slightly more inflated than in Artiodactyla sp. A and the postcingulids and hypoconulids are weak. As such, the range of variation in *D. s.-metsiacus* includes some of the derived features that are increased in the frequency and degree of expression in Artiodactyla sp. A on the one hand and *D. s.-kelleyi* on the other.

Rose (1982) concluded that the skeleton of *Diacodexis* was too specialized for the genus to be ancestral to the Suina and some extinct non-ruminants. However, his observations apply only to two specimens of *D. s.-metsiacus* rather than *Diacodexis* as a whole; skeletal features of *D. s.-metsiacus* may have varied as much as do the dental ones (R. Bakker, personal communication concerning the distal fusion of the tibia and fibula). Also, if skeletal evolution in *Diacodexis* tracked our reconstruction of dental evolution, the skeleton of *D. s.-primus* (unknown) may have been less specialized in some features; in any event, there is no *a priori* reason to assume that its skeleton was as specialized as the two specimens of *D. s.-metsiacus.* If elongate limbs and a fused distal tibia and fibula characterize *D. s.-metsiacus* (Rose, 1982), they should also occur in subsequent lineage segments of *D. secans,* as well as *D. minutus, D. woltonensis,* antiacodontids, homacondontids, and leptochoerids, following our reconstruction of the evolutionary relationships of these taxa based on dental evidence. These features are known in *Antiacodon pygmaeus, Homacodon vagans* (West, 1984), *Leptochoerus* (Marsh, 1894; Edwards, 1976), and *D. minutus* (see below).

←

Fig. 4.—*Diacodexis secans* (lineage segment *D. s.-metsiacus*). (A) AMNH 4696 (cotype of *D. metsiacus*); (B), (D) and (E) AMNH 4700 (holotype of *D. brachystomus*); (C) AMNH 15666; all approx. ×2. Note that the left P^3 in (E) is permanently mounted in the right maxilla.

Table 7.—*Dimensions of lower teeth of* Diacodexis secans, *lineage segment* D. s.-metsiacus.

		P_2		P_3		P_4		M_1		M_2		M_3	
Specimen no.	Locality	L	W	L	W	L	W	L	W	L	W	L	W
AMNH 4700*	Willwood	5.0	1.5	5.6	2.0	4.7	2.8		3.5	4.5	4.0	5.4	3.4
AMNH 4700	Fm.		1.6	5.5		4.5	2.6	4.2	3.4	4.3	3.9	5.5	3.6
AMNH 15666**	Dorsey			5.8	2.2	5.0	2.8		3.4	4.3	4.0	5.4	3.7
AMNH 15666	Creek	5.4	1.9	5.8	2.2	5.1	2.9		3.5	4.3	4.0	5.4	3.7
AMNH 15522	2 mi E	5.5	2.0			5.0	2.7	4.1	3.3	4.3	3.7	5.4	3.4
AMNH 15522	St. Joe					5.0	2.7	4.2	3.2	4.2	3.7	5.1	3.3
UCM 52565	UCM 84248			5.0	2.0	4.4	3.4	4.1	3.1				
UCM 52565	UCM 84248							4.1	3.1	4.3	3.3		
UCM 52551A	UCM 84183					4.8	2.8	4.1	3.1				
UCM 52551B	UCM 84183					4.6	2.7	4.1	3.0		3.5		
UCM 52551C	UCM 84183					4.8	2.6	4.1	3.3				
UCM 52556A	UCM 85258					5.0	2.6			4.7	3.9		
UCM 52556B	UCM 85258					4.9		4.1	3.1	4.6	3.7		
UCM 52558	UCM 84183					4.9	2.8	4.4	3.4	4.6	3.8		
UCM 52560	UCM 84177					5.7	3.1		3.4	4.5	4.1		
UCM 52562A	UCM 84178					4.7	3.0	4.1	3.2	4.4	4.0		
UCM 52562B	UCM 84178					4.7	2.5	4.2	3.3	4.5	3.7		
UCM 52563	UCM 84254					4.7	2.4	4.1	3.0	4.5	3.4		
UCM 52566	UCM 84168					4.8	2.2				3.8	5.2	3.4
UCM 52570	UCM 84178					5.2	2.9	4.2	3.4	4.6	4.0		
UCM 52571	UCM 84249					4.9	3.6	4.5	3.6				
UCM 52571	UCM 84249					5.0	3.6					5.2	3.6
UCM 52572	UCM 84254					5.2	3.0	4.2	3.3	4.4	3.6		
UCM 52573	UCM 84227					5.4	2.5			4.3	3.6	4.8	3.4
UCM 52574	UCM 84178					5.0	2.9	4.1	3.2	4.2	3.8		
UCM 47604	UCM 81092					5.3	2.9	4.1	3.2	4.3	3.8		
UCM 45778	UCM 82022					4.9	2.5	4.2	3.1	4.5	3.7		
CM 58131	CM 843						2.6	3.9	3.4	4.1	4.0	5.4	3.6
CM 58132	CM 843						2.7	4.1	3.2	4.3	3.7		3.3
CM 53912	CM 843					5.2	2.6	4.4	3.5				
CM 12419	CM 673					5.1	2.5	4.3	3.4	4.6	4.2		
CM 12368	CM 147							4.2	3.6	4.5	4.2	5.8	3.8
UCM 52568	UCM 85259							4.3	3.2	4.6	3.6	4.8	3.5
UCM 52578	UCM 84178								3.4	4.6	4.1		3.7
UCM 45783	UCM 80024								3.2	4.2	3.6		
UCM 44123	UCM 80066							4.5	3.2	4.7	3.9		

Table 7.—*Continued.*

Specimen no.	Locality	P_2		P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W	L	W
UCM 44126	UCM 80066							4.2	3.3	4.4	3.6		
UCM 52551E	UCM 84183							4.2	3.5	4.4		5.4	3.5
UCM 52551F	UCM 84183							4.1	3.2	4.3	3.8	5.0	3.5
UCM 52551H	UCM 84183							3.9	3.0				
UCM 52552	UCM 84181							3.7	3.0	4.5	3.6		3.4
UCM 52557	UCM 85260							4.1	3.3	4.2	3.6	4.7	3.2
UCM 52555	UCM 84178								3.0	4.2	3.5	5.0	3.3
UCM 52551D	UCM 84183									4.5	3.8		
UCM 52551G	UCM 84183									4.0	3.8	4.6	3.4
UCM 52554	UCM 84249									4.3	3.5	5.1	3.2
UCM 52559	UCM 85227									4.3	3.6	5.4	3.1
UCM 52561	UCM 84178									4.3	4.0	5.1	3.5
UCM 52564	UCM 84172									4.0	3.2	5.1	3.2
CM 58137	CM 843									4.0	3.6		
CM 58134	CM 843									4.3	3.5		3.4
CM 12395	CM 843									4.2	3.5	5.2	3.3
CM 12396	CM 843									4.6	4.0	5.5	3.5
UCM 52567	UCM 84183									4.5	3.7	5.3	3.4
UCM 52569	UCM 85257									4.6	3.9	5.1	3.5
UCM 52575	UCM 85237										3.6	5.6	3.5
UCM 44128	UCM 80066									4.3	3.3	5.0	2.9
CM 19427	CM 843									4.1	3.7	5.0	3.3
UCM 44127	UCM 80066									4.0	3.4	4.7	4.0
AMNH 4696***	Coryphodon beds									4.1	3.3	5.0	3.2
UCM 52551I	UCM 84183											5.1	3.3
UCM 52551J	UCM 84183											5.4	3.7
UCM 52551K	UCM 84183											5.0	3.4
UCM 52551L	UCM 84183											5.0	3.2
Mean		5.30	1.75	5.54	2.10	4.95	2.79	4.16	3.27	4.36	3.73	5.17	3.43
N		3	4	5	4	28	29	32	39	50	52	34	38

* Holotype of *Diacodexis brachystomus.*

** Plesiotype of *Diacodexis chacensis.*

*** Cotype of *Diacodexis metsiacus.*

Table 8.—*Dimensions of upper teeth of* Diacodexis secans, *lineage segment* D. s.-metsiacus.

		P^3		P^4		M^1		M^2		M^3	
Specimen no.	Locality	L	W	L	W	L	W	L	W	L	W
AMNH 4700*	Willwood		3.3	3.8	4.5	4.4	5.5	4.7	6.3	4.5	6.3
AMNH 4700	Fm.			4.1	4.4	4.4	5.0	4.6	6.3	4.2	5.9
AMNH 15666**	Dorsey Cr			4.1	5.1	4.2	5.2				
UCM 52577	UCM 84255			3.4	4.7	3.9	5.0	4.1	5.6	4.0	5.6
UCM 52567	UCM 84183			3.7	5.0	3.9	5.3	4.3	4.8	3.7	5.1
UCM 52553	UCM 84248			3.8	4.8	4.1	5.2	4.4	5.9		
UCM 52576	UCM 84180							4.6	5.8	4.4	5.8
UCM 52566	UCM 84168							4.2	5.7	3.9	5.6
Mean				3.82	4.75	4.15	5.20	4.41	5.77	4.12	5.72
N				6	6	6	6	7	7	6	6

* Holotype of *Diacodexis brachystomus.*

** Plesiotype of *Diacodexis chacensis.*

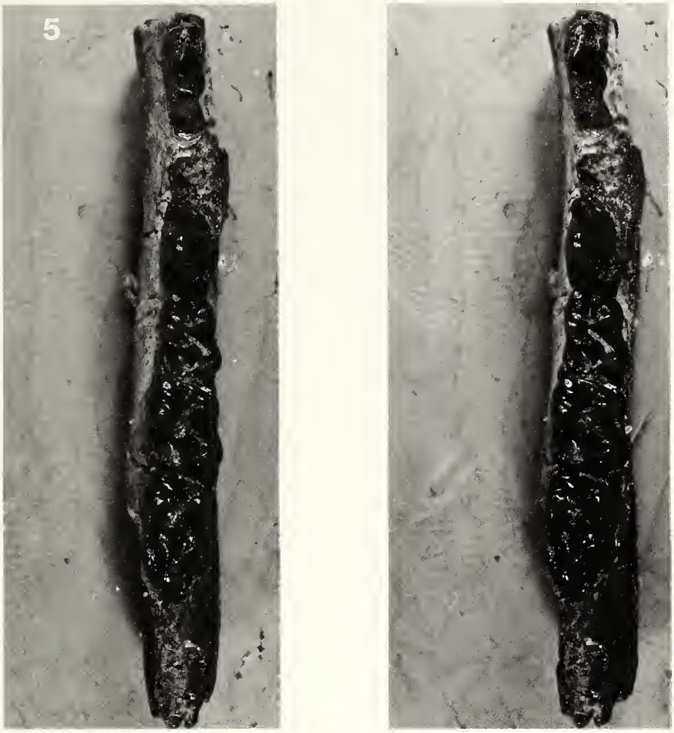


Fig. 5.—*Diacodexis secans* (lineage segment *D. s.-primus*). AMNH 15672; approx. ×2.

Lineage Segment *Diacodexis secans-primus*
(Fig. 5; Tables 1–2, 9–10)

Etymology.—primus, L., first, earliest; in allusion to the earliest known occurrence of *D. secans.*

Diagnosis.—Differs from the other lineage segments of *D. secans* as follows: complete lack of a P_4 postmetacristid, a talonid notch and a postmetacristid on the molars; P_{3-4} shorter; M_{1-3} talonid basin closed lingually by a pre-entocristid; M_3 usually longer with an elongate hypoconulid lobe; more frequent occurrence of a partial or complete hypoconid-entoconid connection on M_3; molar paraconids directly anterior to metaconids; compared to *D. s.-kelleyi* and *D. s.-secans,* P^3 protocone weaker, with metacone (when present) closer to metastyle; P_3 shorter than M_3, molar protocones less inflated with more distinct protocristae, conulecristae, conules and pseudohypocones.

Diagnostic series.—CM 12258, 36810; AMNH 15527, 15671, 15672; UCM 19388, 38121, 49404; UW 7544, 7571, 9213.

Table 9.—*Dimensions of lower teeth of* Diacodexis secans, *lineage segment* D. s.-primus.

Specimen no.	Locality	P_2		P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W	L	W
CM 36805	CM 878	3.0	1.5										
AMNH 15672	Shoshone R.	4.0	1.6			4.4	2.7	4.0	3.2	4.6	3.9	6.0	3.9
AMNH 15527*	Elk Cr			4.8	1.7	4.6	2.4	4.0	3.0	4.4	3.7	6.0	3.6
CM 17472	CM 681			4.9	2.0	5.0	2.8	4.2	3.4				
UW 7571	UW 37			4.7	1.9	4.7	2.5	4.1	3.3	4.3	4.0	6.2	4.0
UW 7544	UW 28					4.4	2.3	4.2	2.9	4.7	3.7	6.0	3.8
CM 57693	CM 878				1.7	4.8	2.5	4.0	3.2				
UCM 49403	UCM 81003			5.0	1.9								
UCM 52579	UCM 84195					4.5	2.9			4.3		5.0	3.5
CM 12244	CM 140					4.8	2.4	4.2	3.3				
CM 12291	CM 678					4.6	2.4		3.1				
CM 34338	CM 141					4.9	2.4						
CM 34363	CM 187					4.7	2.5						
CM 36653	CM 878						2.7		3.3	4.7	3.9		
CM 57694	CM 878					4.8	2.7						
UCM 19388	Elk Cr					4.5	2.2	4.0	2.9	4.5	4.2	6.0	4.0
UCM 49410	UCM 81003					5.0	2.4						
CM 39361	CM 953					4.2	2.2						
CM 39361	CM 953					4.4	2.4						
CM 39360	CM 953					4.3	2.2						
CM 39360	CM 953					4.3	2.1						
CM 12188	CM 150								3.3	4.2	3.8	6.0	3.8
CM 34310	CM 142							4.1	3.1	4.7	3.9		
CM 36186	CM 878								3.4	4.6	4.0		
UCM 19468	CM 187								3.0	4.3	3.9	5.9	3.6
UCM 20934	CM 187							3.9	3.3	4.6	4.0		
UCM 49408	UCM 81003							4.2	3.4				
UCM 49406	UCM 81003							4.0	3.0				
UCM 49407	UCM 81003							4.2	3.2				
UCM 49402	UCM 81003							4.3	3.3				

Table 9.—*Continued.*

Specimen no.	Locality	P_2		P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W	L	W
UCM 49401	UCM 81003							4.2	3.3				
CM 38873	CM 953							4.1	3.2	4.3	3.8		
CM 38872	CM 953							3.8	3.0				
CM 38874	CM 953							4.0	3.1				
CM 38871	CM 953							4.0	2.9				
CM 34351	CM 678							3.9		4.5	3.8		
CM 36181	CM 878								3.1	4.4	3.6		
UCM 52581	UCM 84195									4.5	4.1		4.0
CM 36817	CM 878									5.0	4.1	5.8	4.0
CM 12207	CM 154									4.4	4.0	6.0	4.0
CM 12167	CM 149									4.6	3.8	6.1	3.9
CM 12227	CM 187									4.3	3.9	5.5	3.5
CM 12260	CM 140									4.4	3.8	6.0	3.5
CM 12259	CM 140									4.7	3.9	6.1	3.8
CM 12258	CM 140									4.4	3.8	5.4	3.5
CM 17470	CM 681									4.6	3.9	6.3	4.0
CM 36207	CM 878										3.5	5.5	3.5
CM 36213	CM 878										3.9	5.7	3.7
CM 36650	CM 878									4.7	3.9		
CM 36708	CM 878									5.0	4.1		
CM 36807	CM 878									4.4	3.8		
CM 36810	CM 878									4.7	3.8	5.8	3.6
CM 36811	CM 878									4.5	4.0		
CM 36812	CM 878									4.3	3.6		
CM 58136	CM 1093										4.1	5.8	4.0
CM 58135	CM 1093									4.3	4.0	5.6	3.8
UCM 19393	CM 677									4.0	4.2		
UCM 49404	UCM 81003									4.9	4.1		
UCM 49400	UCM 81003									4.5	3.9		

Table 9.—*Continued.*

Specimen no.	Locality	P_2 L	P_2 W	P_3 L	P_3 W	P_4 L	P_4 W	M_1 L	M_1 W	M_2 L	M_2 W	M_3 L	M_3 W
UCM 49397	UCM 81002									4.5			
UCM 49413	UCM 83198									4.5	3.7		
UCM 49414	UCM 83198									4.9	3.7		
CM 38874	CM 953									4.2	3.6		
CM 38874	CM 953									4.4	3.8		
CM 12231	CM 153									4.7	4.1		
UCM 52580	UCM 84198											6.7	4.2
UCM 52580	UCM 84198											5.7	3.9
CM 28957	CM 157											5.9	3.7
CM 34325	CM 678											5.6	3.6
CM 36183	CM 878											6.2	3.9
CM 36185	CM 878											5.4	3.6
CM 36182	CM 878											5.7	3.8
CM 36209	CM 878											5.2	3.5
CM 36212	CM 878											5.6	3.8
CM 36651	CM 878											5.9	3.7
CM 37434	CM 878											5.9	3.7
CM 37433	CM 878											6.3	
CM 37436	CM 878											5.6	4.1
CM 38127	CM 878											6.7	
CM 36604	CM 878												3.4
UCM 40352	CM 187											5.5	3.7
UCM 49399	UCM 81003											5.5	3.5
UCM 49136	UCM 81002											5.8	3.7
CM 38876	CM 953											5.5	3.5
Mean				4.85	1.84	4.61	2.46	4.07	3.17	4.51	3.89	5.83	3.75
N				4	5	18	19	20	25	40	41	39	39

* "Plesiotype" of *Diacodexis chacensis.*

Referred specimens.—In addition to material referred elsewhere (McKenna, 1960; Delson, 1971; Bown, 1979), CM 12167, 12188, 12207, 12227, 12231, 12244, 12258–12260, 12291, 12301, 17467, 17470, 17472, 28956, 28957, 28974, 34310, 34325, 34338, 34351, 34363, 36175, 36177, 36179, 36181–36183, 36185, 36186, 36204, 36207–36213, 36602–36604, 36650, 36651, 36653, 36708, 36801–36805, 36807–36814, 36816, 36817, 36870, 37433–37436, 37438, 37439, 38126–38129, 38865–38876, 39360, 39361, 53709, 53724, 57693, 57694, 58135, 58136; AMNH 15527, 15671, 15672; UCM 19388, 19393, 19468, 20934, 38121, 40352, 49136, 49137, 49397, 49399–49411, 49413, 49414, 52579–52581; UW 7544, 7571, 7577, 9215, 9996.

Localities.—CM loc. 953 (Sandcouleean, Wasatch Fm.), Colorado. UCM locs. 81003, 81002, 83198 (Sandcouleean—early Graybullian, "Wasatch Fm."), Wyoming. CM locs. 140, 141, 142, 149, 150, 153, 154, 157, 187, 676, 677, 678, 681, 878, 909, 1093; AMNH locs. Elk Creek, Tenmile Creek, 3 miles S. of Shoshone R.; UCM locs. 84195, 84198; UW locs. 28, 34, 37, 38, 55 (Sandcouleean—early Graybullian, Willwood Fm.), Wyoming.

Known distribution.—Early Wasatchian (Sandcouleean—early Graybullian)—Bighorn Basin (Willwood Fm.) and Powder River Basin ("Wasatch Fm."), Wyoming; earliest Wasatchian (Sandcouleean)—Four Mile area (Wasatch Fm.), Colorado.

Discussion.—*D. s.-primus* is the earliest known lineage segment of *D. secans* and the most primitive in features treated above in the diagnoses and discussions of the other lineage segments. Dentally, it is also the most primitive known artiodactyl. It is most distinct from the other lineage segments in lacking a postmetacristid on all known P_4s, and a talonid notch and a postmetacristid on the molars, and in having an unreduced molar paraconid directly anterior to the metaconid. P^3 have a weak protocone either directly lingual to the paracone or slightly posterior; some have an incipient metacone on the postparacrista near the metastyle.

Apart from its degree of morphologic overlap with *D. s.-metsiacus,* the most variable feature in *D. s.-primus* is the morphology of the hypocristid on M_3. On eight of the M_3s ($n = 33$) the hypocristid divides into two forks, one of which extends to the hypoconulid and the other partly or completely to the entoconid. This feature also occurs on one M_3 of Artiodactyla sp. A (UCM 47891; $n = 11$), Artiodactyla sp. B, (CM 43133; $n = 1$), *D. s.-metsiacus* (UCM 19427; $n = 35$), *D. s.-kelleyi* (CM 22816; $n = 47$) and one figured M_3 of the European *D. gazini* (Sudre et al., 1983). Among non-diacodexeids, a partial or complete connection between the entoconid and hypoconid occurs in antiacodontids and homacodontids. Other derived characters shared by the latter clades (elevation of conjoined paraconid and metaconid on M_{1-3}; non-inflation of metaconid; conical entoconid isolated from hypoconulid and as tall as the hypoconid; broad postcingulid; strong hypoconulid and hypocristid) do not occur in *D. s.-primus* but, in part, do

Table 10.—*Dimensions of upper teeth of* Diacodexis secans, *lineage segment* D. s.-primus.

		P^3		P^4		M^1		M^2		M^3	
Specimen no.	Locality	L	W	L	W	L	W	L	W	L	W
AMNH 15671	10 Mile Cr	5.6	3.7	3.5	4.6	4.1	5.0	4.1	6.0	4.0	5.9
UCM 52579	UCM 84195	5.1		3.7	4.4	3.9	5.1	4.2	4.9		
CM 17467	CM 681			3.4	4.7	4.0	4.9				
UCM 38121	BHB			3.9	5.0	4.1	5.2	4.2	5.6	3.9	5.4
CM 36813	CM 878			4.0	4.5						
CM 12301	CM 676					3.9	5.0	4.4	5.7	4.6	6.0
CM 36814	CM 878					4.0		4.4	5.9	4.4	6.0
UW 9215	UW 38					4.2	4.8	4.6	5.8	4.3	6.0
CM 38865	CM 953					3.8	5.2				
CM 38865	CM 953					4.0	4.9				
CM 38865	CM 953					3.6	4.6				
CM 28974	CM 909					4.0	5.4				
CM 36175	CM 878					4.0					
CM 36179	CM 878					3.8	5.0				
CM 36210	CM 878					4.1	5.2				
CM 36809	CM 878					3.7	4.8				
CM 36801	CM 878					3.9	4.8				
CM 37438	CM 878					4.0	4.8				
UCM 49137	UCM 81002					3.8	5.4				
CM 28956	CM 157							4.5	6.2		

Table 10.—*Continued.*

Specimen no.	Locality	P^3		P^4		M^1		M^2		M^3	
		L	W	L	W	L	W	L	W	L	W
CM 36211	CM 878							4.5	5.8		
CM 36804	CM 878							4.3	5.6		
CM 36816	CM 878							4.3	5.4		
CM 37435	CM 878							4.5	5.7		
UCM 49405	UCM 81003							4.7	5.9		
CM 53709	CM 1093								5.8		
CM 38866	CM 953							4.0	5.6		
CM 38866	CM 953							4.0	5.3		
CM 38867	CM 953							4.3	5.6		
CM 38869	CM 953									3.5	5.0
CM 38868	CM 953									4.0	5.1
CM 36177	CM 878									4.1	5.6
CM 36208	CM 878									4.2	5.5
CM 36602	CM 878									4.0	5.8
CM 36808	CM 878									4.5	5.7
CM 37439	CM 878									4.5	5.5
CM 53724	CM 1093									3.8	5.2
Mean				3.70	4.64	3.94	5.01	4.33	5.68	4.14	5.59
N				5	5	18	16	15	16	13	13

describe the morphology of Artiodactyla sp. A and sp. B (see below) and some material of *D. s.-metsiacus.* As such, the frequency of occurrence of the partial or complete hypoconid-entoconid connection on M$_3$ in *D. s.-primus* and *D. s.-metsiacus* may imply their ancestral position with regard to Artiodactyla sp. A and sp. B, antiacodontids and homacodontids. Such a conclusion agrees with the temporal occurrence of these taxa and, more importantly, with the retention of primitive features in antiacodontids and homacodontids (short P$_{3-4}$; elongate hypoconulid lobe on M$_3$; strong molar conules and conulecristae) that are modified in more derived lineage segments of *D. secans.* Two upper molars of *D. s.-primus* from Four Mile are *Antiacodon*-like in the separation of the metaconule from the protocone, the deep trigon basin, the well-developed pseudohypocone, the strong conulecristae, and the nearly complete lingual cingulum.

Diacodexis minutus, new species

(Fig. 6; Tables 1–2, 11–12)

Diacodexis chacensis, Robinson, 1966:69.
Diacodexis metsiacus, Guthrie, 1971:85 in part.

Etymology.—*minutus,* L., small; in allusion to the small size of this species.

Holotype.—CM 22512, left P$_4$–M$_3$, from CM loc. 34, Lost Cabin Member, Wind River Formation, Wind River Basin, Wyoming.

Diagnosis.—Smaller and less robust than the penecontemporaneous lineage segment of *D. secans* (*D. s.-secans*), and less robust and M$_2$ smaller than *D. woltonensis,* with molar cusps (especially metaconid) much less inflated, talonid basins deeper, cristae and conules more distinct. Unlike Artiodactyla sp. A and sp. B and *D. gracilis,* molar trigonids not as compressed anteroposteriorly, lower molars with strong talonid notch and postmetacristid and with more inflated cusps; paraconid usually less medial and less reduced than in *D. gracilis*; metaconid-paraconid wall not as elevated as in Artiodactyla sp. A and sp. B.

Syntypic series.—CM 21132, 21142, 22538, 22593, 27475, 27459, 36443, 36446, 37311, 37313, 40765, 40769, 40774, 43712, 43713, 55138, 55152; UCM 46808; AMNH 17552, 92879, 96479; PU 13430.

Referred specimens.—CM 20982, 20989, 20992, 20994, 21000, 21013, 21075, 21098, 21129, 21130, 21132, 21142, 21928, 22538, 22593, 27459, 27460, 30953, 30989, 31002, 31010, 35786–35791, 36417, 36443, 36446, 37305, 37306, 37309–37313, 40765, 40767–40769, 40771, 40774, 40775, 42071, 42072, 42118, 43192, 43193, 43473, 43706, 43709, 43710, 43712, 43713, 44845, 44907, 44913, 55135–55139, 55152–55155, 55157, 55159, 55363, 55367; AMNH 17552, 92879, 94472, 96479; UCM 46808, 45516, 44401 (tentatively); PU 13430, 18344.

Localities.—AMNH loc. Huerfano 6 (Lostcabinian, Huerfano Fm.); CM loc. 1046, AMNH loc. Alkali Creek (Lostcabinian, Lost Cabin

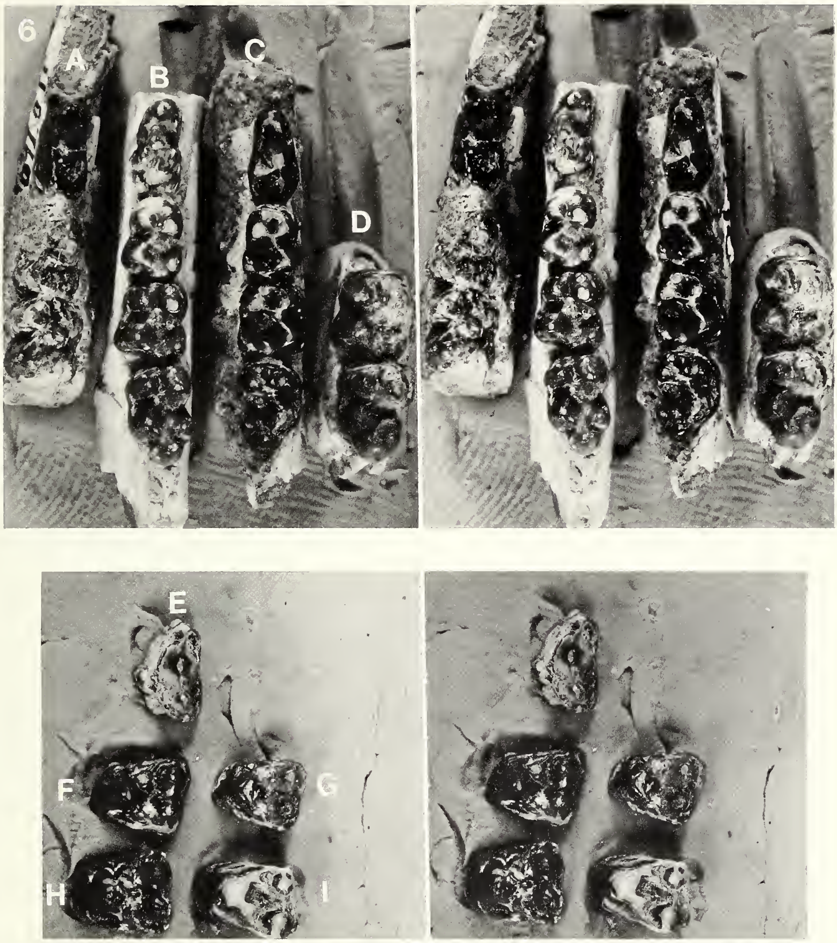


Fig. 6.—*Diacodexis minutus,* new species. (A) CM 40769; (B) CM 22512, holotype; (C) CM 55152; (D) CM 40774; showing range of variation in the lower teeth. (E) CM 44913, P^3; (F) CM 55139, M^1; (G) UCM 46808, M^1; (H) UCM 44401, M^2; (I) CM 43712, M^2. All approx. ×2.

Mbr., Wind River Fm.); UCM loc. 80062 (Lostcabinian, Red Creek facies, Wind River Fm.); CM locs. 34, 1036, 1078, UCM loc. 81027 (Gardnerbuttean, Lost Cabin Mbr., Wind River Fm.).

Known distribution.—Late Wasatchian (Lostcabinian)—Huerfano Basin (Huerfano Fm.), Colorado; late Wasatchian to early Bridgerian

Table 11.—*Dimensions of lower teeth of* Diacodexis minutus *from the Wind River Formation, Wyoming.*

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 43192	CM 34	5.2	1.7	4.7	2.1						
CM 21130	CM 34	5.4	2.0								
CM 37313	CM 34	5.0	1.8	4.2	2.4	3.7	2.8	3.8	3.4		
CM 37312	CM 34			4.7	2.5	4.0	3.1	4.0	3.6		
CM 22512*	CM 34			4.5	2.4						
CM 22512*	CM 34			4.7	2.8	3.8		3.9	3.3	4.9	3.1
CM 43473	CM 34			4.5	2.5						
CM 55136	CM 34			4.2	2.3						
CM 55363	CM 34			4.8	2.6						
CM 55137	CM 34			4.7	2.5	3.8	3.2				
CM 21129	CM 34			4.8	2.6						
CM 21013	CM 34			4.6	2.5						
CM 40767	CM 34			4.7	2.6	3.6	3.0	4.0	3.4		
CM 40769	CM 34			4.7	2.5		3.1	4.0	3.5		
CM 20989	CM 34			4.2	2.3	3.8	3.0	3.8	3.4		
CM 21000	CM 34			4.6	2.5	3.8	3.1				
CM 20982	CM 34			4.4	2.3	3.7					
CM 43193	CM 1078			4.1	2.0						
CM 30989	CM 34			5.0	2.8						
CM 27459	CM 34			4.7	2.7	3.7	3.1	4.0	3.2		
CM 55152	CM 34			4.6	2.5	3.7	2.9	3.8	3.1	4.5	3.2
AMNH 17552	Huerfano 6			4.2	2.1	4.0	3.0	4.4	3.5		
AMNH 92879	CM 1046			4.5	2.5			4.2	3.5	4.8	3.2
PU 13430	CM 34			4.8	2.7	4.1	3.3	4.1	3.5		
PU 18344	CM 34					3.8	3.0	3.9	3.1		
CM 55157	CM 34					3.7	3.0	3.7		4.7	3.2
CM 55153	CM 34					3.9	3.3				
CM 55367	CM 34					4.0	3.0	3.9	3.3		
CM 55159	CM 34					3.8	3.1				
CM 55155	CM 34					4.4	3.5				

Table 11.—*Continued.*

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 42071	CM 34					3.9	2.8				
CM 37311	CM 34						3.1	4.0	3.4		
CM 37306	CM 34					4.0	3.3				
CM 44914	CM 34					3.8	3.0				
CM 40765	CM 34					3.8	3.0	4.2	3.5		
CM 31002	CM 34					3.7	3.1	3.8	3.5	4.9	3.2
CM 22538	CM 34					4.1	3.1				
CM 42118	CM 34					3.9	3.0				
CM 43710	CM 34					3.8	3.0				
AMNH 96479	Alkali Cr.					3.7	2.6				
CM 42072	CM 34							4.1	3.4	4.9	3.4
CM 30953	CM 34							4.1	3.2		
CM 37309	CM 34							4.1	3.6	5.1	3.5
CM 21132	CM 34							4.2	3.3		3.2
CM 40774	CM 34							4.3	3.5	4.8	3.1
CM 40771	CM 34							4.0	3.4	4.6	3.2
CM 40768	CM 34							3.8	3.4	4.6	3.2
CM 21142	CM 34							3.8	3.2	4.5	3.0
CM 36417	CM 34							4.2	3.5		
CM 40775	CM 34							3.9	3.3	4.8	3.0
AMNH 94472	Huerfano 6							4.4	3.5		
CM 43706	CM 34							4.0	3.5	5.4	3.5
CM 31010	CM 34							3.9	3.4	4.8	3.1
CM 27460	CM 34							3.8	3.6	4.8	3.2
CM 20994	CM 34								3.5	4.8	3.1
CM 55135	CM 34							4.2	3.3		
CM 55138	CM 34							4.2	3.6	5.0	3.6
CM 22593	CM 34							4.2	3.3	4.8	3.4
CM 21075	CM 34									4.9	3.1

Table 11.—*Continued.*

Specimen no.	Locality	P_3 L	P_3 W	P_4 L	P_4 W	M_1 L	M_1 W	M_2 L	M_2 W	M_3 L	M_3 W
CM 21928	CM 34									4.8	3.2
CM 43709	CM 34									5.0	3.3
CM 44845	CM 1036									4.7	3.1
CM 21098	CM 34									4.9	3.1
CM 37305	CM 34									4.6	3.5
CM 35791	CM 34									4.7	2.9
CM 20992	CM 34									5.0	3.4
Mean		5.20	1.83	4.56	2.47	3.85	3.06	4.02	3.40	4.82	3.22
N		3	3	23	23	27	27	34	34	26	27

* Holotype of *D. minutus.*

(Lostcabinian—Gardnerbuttean)—Wind River Basin (Wind River Fm.), Wyoming.

Discussion.—P^4 and teeth anterior to $P^3/_3$ are unknown. The dentition of *D. minutus* is smaller and more gracile than that of *D. s.-secans, D. s.-primus,* most specimens of *D. s.-kelleyi* and *D. woltonensis,* and many specimens of *D. s.-metsiacus.* It is closest in size to some specimens of *D. s.-metsiacus,* Artiodactyla sp. A, *D. gracilis,* and three specimens of *D. s.-kelleyi,* but can be distinguished from these groups by the following suite of features: elongate P_3; strong postmetacristid on P_4–M_3; deep talonid basin and well-developed talonid notch on M_{1-3}. Additionally, the molar trigonids are not as compressed anteroposteriorly as in Artiodactyla sp. A and *D. gracilis,* the paraconid is not as reduced and medial as in *D. gracilis,* and the trigonid not as elevated as in Artiodactyla sp. A.

D. minutus occurs penecontemporaneously and in lithosympatry in the Lostcabinian with *D. s.-secans* and *D. woltonensis* and in lithosympatry with *D. s.-secans* at the Gardnerbuttean CM loc. 34. Compared to these groups, the teeth in *D. minutus* are smaller, P_4 almost invariably has a postmetacristid, M_{1-2} are less nearly square, the molar metaconids are usually much less inflated, the protoconids and hypoconids are less bulbous, the talonid basins are deeper and the hypoconulid and entoconid often share a common wall. Derived features shared with *D. s.-secans* and *D. woltonensis* are the high frequency of occurrence of a well-developed molar postmetacristid and talonid notch; these morphoclinal features may imply the common ancestry of *D. s.-secans, D. woltonensis* and *D. minutus* from *D. s.-kelleyi,* specimens of which approach and overlap the former taxa in these features. Indeed, three of the smallest specimens assigned to *D. s.-kelleyi* (CM 39221, 54212, 44906) may represent either Lysitean *D. minutus* or that part of the variation of *D. s.-kelleyi* that was canalized in *D. minutus.* Other derived (and morphoclinal) features, such as robusticity of the molars (especially the metaconid) also link *D. s.-secans* and *D. woltonensis* with *D. s.-kelleyi.*

Alternatively, *D. minutus* may be more closely related to the *D. s.-metsiacus* segment of the *D. secans* lineage, molars of which also bear a postmetacristid and talonid notch (although they are weaker and occur at a lower frequency) as well as a more gracile metaconid (some specimens), as in *D. minutus.*

The problem of reconstructing the specific evolutionary relationships of *D. minutus* is grounded in the non-digital nature of the derived character states, namely, a series of temporal morphoclines that first appear in *D. s.-metsiacus,* increase in the frequency and degree of expression in *D. s.-kelleyi,* and more so in *D. s.-secans, D. woltonensis,*

Table 12.—*Dimensions of lower teeth of Artiodactyla sp. A, Artiodactyla sp. B, and* Diacodexis gracilis.

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
				Artiodactyla sp. A							
CM 43135	CM 941		1.5	4.9	2.1						
CM 43129	CM 945			4.5	2.1						
UCM 48526	UCM 78049			4.1	2.3	3.7	2.8	4.0	3.4		
UCM 47053	UCM 78049						2.8	4.0	3.3	4.8	2.8
CM 43132	CM 941						2.7	4.1	3.2		
CM 10475	Indian						2.9	4.2	3.5	5.1	3.1
CM 10475	Valley					4.2	2.8	4.2	3.3		
CM 43702	Scenery Gulch								3.4	4.8	3.2
CM 43130	CM 1017									5.2	3.2
UCM 47052	UCM 78049							4.2	3.6	4.9	3.3
AMNH 16296	Ojo San Jose E. Bluff							4.3	3.4	5.2	3.1
CM 43134	CM 1017									4.7	2.9
UCM 47891	UCM 78049									5.0	3.1
UCM 40831	UCM 78033									5.0	3.1
Mean				4.50	2.17	3.95	2.80	4.14	3.39	4.97	3.09
N				3	3	2	5	7	8	9	9
				Artiodactyla sp. B							
CM 43133	CM 941					4.4	3.2	5.0	3.7	6.4	3.6
CM 43128	CM 941							4.8	3.2		
AMNH 237	GGS 1949									6.2	3.6
AMNH 86289	GGS 1937							4.7	3.7	5.9	3.7
Mean								4.83	3.53	6.17	3.63
				Diacodexis gracilis							
UCM 52582*	UCM 84255			4.0	2.2	3.8	2.8	3.7	3.8	4.8	3.0
UCM 52583	UCM 84180			3.9	2.3	3.7	2.8	3.9	3.3		
UCM 52584	UCM 84250					3.8	2.8	3.9	3.3	4.5	3.0
Mean				3.95	2.25	3.77	2.80	3.83	3.47	4.65	3.00

* Holotype.

and *D. minutus.* Furthermore, each of these characters varies continuously in *D. s.-metsiacus* and *D. s.-kelleyi.* As such, there are two acceptable conclusions: (1) *D. minutus* shared an immediate common ancestry with *D. s.-secans* and *D. woltonensis* from *D. s.-kelleyi,* in which case the terminal expression of the morphoclines in the three descendant groups is due to direct descent; (2) *D. minutus* shared an immediate common ancestry with *D. s.-kelleyi* from *D. s.-metsiacus,* in which case the terminal expression of the morphoclines in *D. minutus* on the one hand and *D. s.-secans* and *D. woltonensis* on the other are due to parallelism. Lower molars of *D. s.-secans* and *D. woltonensis* bear greatly inflated metaconids (the terminal expression of another morphocline). The metaconid is usually gracile in *D. minutus,* but is inflated in some Gardnerbuttean specimens (CM 40765, 22593, 22538, 40769, 40774) of this species and approaches the condition in *D. woltonensis* and some Gardnerbuttean specimens of *D. s.-secans* (especially CM 22504). Similarly, the degree of inflation of the molar metaconid is variable in *D. s.-kelleyi* and overlaps at the extremes of the distribution with *D. minutus* on the one hand and *D. s.-secans* and *D. woltonensis* on the other. Such a pattern of variation can also imply either parallelism or direct descent. In sum *D. minutus, D. woltonensis,* and *D. s.-secans* appear to have shared a common ancestry from either the same (*D. s.-kelleyi*) or two different lineage segments (*D. s.-metsiacus, D. s.-kelleyi*) of *D. secans.* This kind and degree of variation in evolving morphoclines has been noted in other taxa with a good fossil record (Gingerich and Simons, 1977).

Two other variable features of note in *D. minutus* are the position and strength of the molar paraconid and the presence of a metaconid on P_4. The paraconid on M_{1-3} is usually small and slightly medial relative to the metaconid, but can be much reduced (M_3 in CM 20992, 22593; M_{1-2} in CM 21132) and quite medial (M_2 in CM 37311, 37312). The metaconid, absent on all but two P_4s, is almost as strong as the protoconid on CM 55152 and is incipient on CM 40769. One M_1 (CM 22538) is unique in having a fused entoconid and hypoconulid.

The few known upper molars of *D. minutus* are much smaller and less robust than those of *D. s.-secans* and most specimens of *D. s.-kelleyi,* and more closely resemble those of *D. s.-metsiacus* in the lack of inflation of the protocone and conules, and the more distinct conulecristae and pseudohypocone. Premetaconulecristae are usually weak or absent.

One specimen of *D. minutus* (CM 44907) preserves a fused distal tibia and fibula. This condition is not surprising, given its occurrence in the more primitive *D. secans* (lineage segment *D. s.-metsiacus*; Rose, 1982), and other apparent sister taxa of the latter—leptochoerids, antiacodontids, and homacodontids. It should also occur in more derived lineage segments of *D. secans* and in *D. woltonensis.*

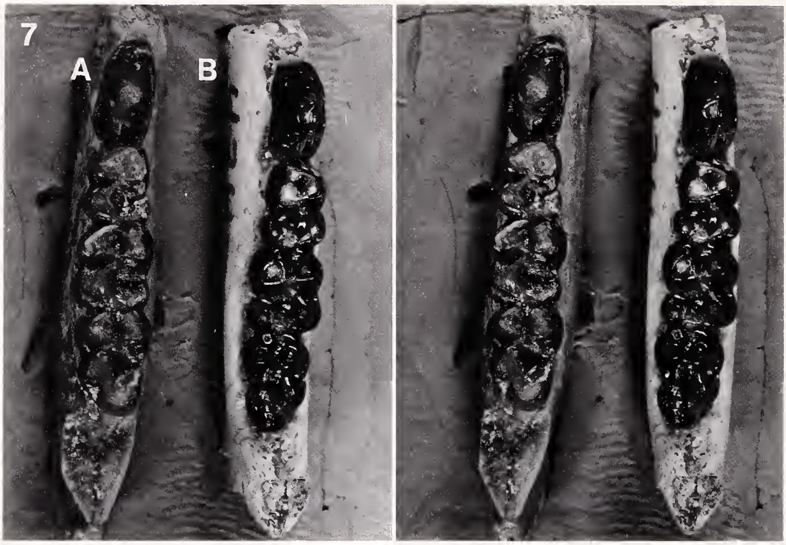


Fig. 7.—*Diacodexis woltonensis,* new species. (A) CM 43474; (B) CM 43478, holotype; both approx. ×2.

Diacodexis woltonensis, new species
(Fig. 7; Tables 1, 13)

Diacodexis metsiacus, Guthrie, 1971:85, in part.

Etymology.—After the now extinct village of Wolton, Wyoming, near Alkali Creek in the Wind River Basin.

Holotype.—CM 43478, right P_4–M_3, from CM loc. 1077, Lost Cabin Member, Wind River Formation, Wyoming.

Diagnosis.—Most robust species of *Diacodexis* in proportion to size, with nearly square M_{1-2}, hyperinflated metaconid, swollen protoconid and hypoconid, small talonid basin; additionally differs from *D. gracilis* and Artiodactyla sp. A and sp. B in having a strong talonid notch and postmetacristid on the lower molars, and a non-compressed trigonid.

Syntypic series and referred specimens.—CM 22592, 40783, 42090–42092, 43474; AMNH 92871; UCM 44423, 44696, 46810.

Localities.—CM locs. 91, 1041, 1042, 1046, 1077 (Lostcabinian, Lost Cabin Mbr., Wind River Fm.); UCM loc. 80062 (Lostcabinian, Red Creek Facies, Wind River Fm.).

Known distribution.—Late Wasatchian (Lostcabinian)—Wind River Basin (Wind River Fm.), Wyoming.

Discussion.—*D. woltonensis* occurs in lithosympatry with *D. s.-secans* (at many localities) and *D. minutus* (at one locality) in the Lost-

Table 13.—*Dimensions of lower teeth of* Diacodexis woltonensis *from the Wind River Formation, Wyoming.*

Specimen no.	Locality	P_3		P_4		M_1		M_2		M_3	
		L	W	L	W	L	W	L	W	L	W
CM 42092	CM 1041		2.4	5.0	2.8						
CM 42090	CM 1042			5.5	3.1					5.6	3.9
CM 42090	CM 1042			5.7	3.1			4.2	3.9		
CM 43474	CM 1046			5.3	2.7	4.0	3.2	4.2	3.7	5.2	3.7
CM 43478*	CM 1077			5.1	2.6	4.2	3.3	4.2	3.7	4.9	3.4
AMNH 92871	WRB			5.5	2.7			4.3	3.7		
CM 40783	CM 1041					4.3	3.4	4.2	4.0	5.2	4.0
UCM 44423	UCM 80062					4.0	3.4				
UCM 44696	UCM 80062					4.2	3.3				
CM 42091	CM 1041							4.3	3.8	5.3	3.7
CM 22592	CM 91							4.1	3.5	5.1	3.4
UCM 46810	UCM 80062									5.6	3.8
Mean				5.35	2.83	4.14	3.32	4.21	3.76	5.27	3.70
N				6	6	5	5	7	7	7	7

* Holotype.

cabinian part of the Wind River Basin, where it is smaller (no overlap) than the former and much more robust and slightly larger (mean size) than the latter (Fig. 13). Specifically, M_{1-3} of *D. woltonensis,* unlike *D. minutus,* bear a hyperinflated metaconid, swollen protoconid and hypoconid, a larger hypoconulid, and a smaller talonid basin. Like *D. s.-secans* and *D. minutus,* lower molars of *D. woltonensis* have a strong postmetacristid and talonid notch, features which, as discussed above (see *D. minutus*), may imply their common ancestry from *D. s.-kelleyi* or may have developed in parallel in *D. minutus* from *D. s.-metsiacus.* In either case, these derived features, as well as the increased robusticity of the molars, are shared by *D. woltonensis* and *D. s.-secans* and imply their common ancestry from *D. s.-kelleyi.*

Although Lostcabinian samples of *D. woltonensis, D. minutus,* and *D. s.-secans* are discrete, Lostcabinian *D. woltonensis* overlaps in size and robusticity of the lower molars and inflation of the metaconid with a few specimens of both Gardnerbuttean *D. minutus* (CM 40774, 40769) and *D. s.-secans* (especially CM 22504) from CM loc. 34. Importantly, these specimens comprise, respectively, the upper and lower extremes of the normal distribution of these two species; also, the mean size of Lostcabinian *D. woltonensis* is intermediate between that of Gardnerbuttean *D. minutus* and *D. s.-secans.*

Our recognition of *D. woltonensis* as a discrete species is based on its clear morphological distinction from lithosympatric Lostcabinian samples of *D. s.-secans* and penecontemporaneous (and lithosympatric) samples of *D. minutus.* Given this systematic interpretation, the pattern of morphological overlap in the Gardnerbuttean may be explained by the local extinction of *D. woltonensis* and consequent expansion of the range of variation of *D. minutus* and *D. s.-secans* toward the size and robusticity of *D. woltonensis.* Other systematic interpretations of the Lostcabinian and Gardnerbuttean material are possible, and may become more evident and tenable with a larger sample size of *Diacodexis,* especially from the Lostcabinian. For example, the Lostcabinian material referred to *D. minutus* may represent the more gracile part of the range of variation of *D. woltonensis.* Alternatively, *D. woltonensis* may represent the more robust part of the range of variation of Lostcabinian *D. minutus.* The few Gardnerbuttean specimens of *D. minutus* and *D. s.-secans* that closely resemble Lostcabinian *D. woltonensis* may represent that species. Any of these hypotheses, if corroborated by further collecting, would alter our reconstruction of the relationships of these taxa. However, the current record and its morphological patterns support the recognition and co-occurence of three species of *Diacodexis* in the Lostcabinian and two in the Gardnerbuttean.

Variable features in *D. woltonensis* include size of M_3, and develop-

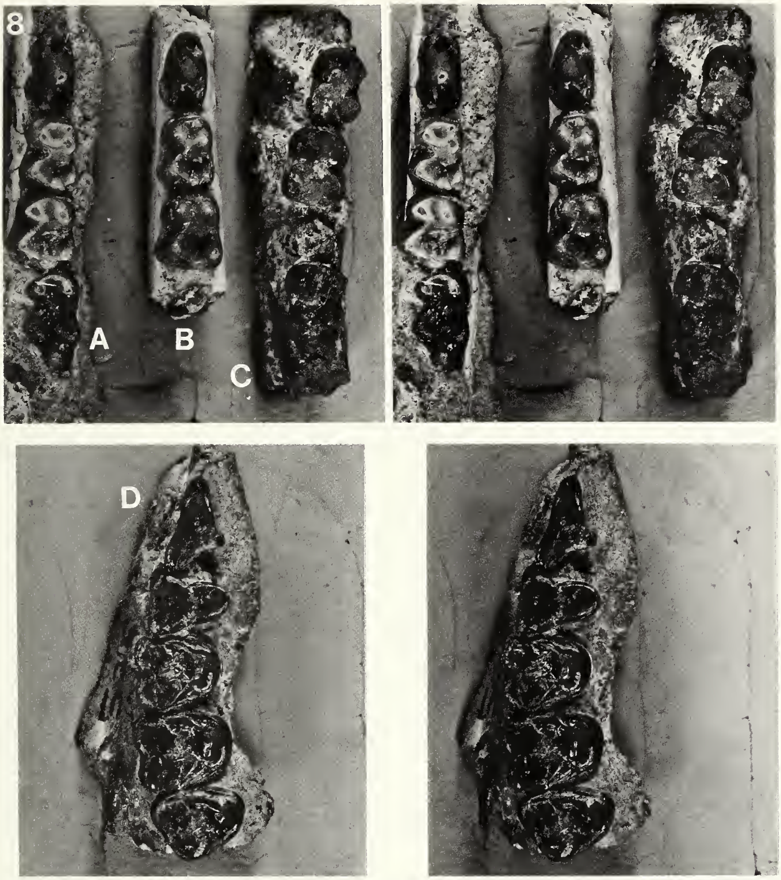


Fig. 8.—*Diacodexis gracilis,* new species. (A) UCM 52582, holotype; (B) UCM 52583; (C) UCM 52584; (D) UCM 52585; all approx. ×2.

ment of the paraconid on the lower molars and especially P_4, where it can be extremely weak or as large as in *D. secans* and *D. minutus.*

Diacodexis gracilis, new species, Krishtalka, Stucky, and Bakker
(Fig. 8; Tables 1–2, 12, 14)

Etymology.—*gracilis,* L., in allusion to the gracile morphology of the dentition.

Holotype.—UCM 52582, left P_4–M_3, from UCM loc. 84255, Willwood Formation, Bighorn Basin, Wyoming.

Diagnosis.—Smallest and most gracile species of *Diacodexis,* with most reduced and medial paraconid on M_{2-3}, most gracile metaconid

Table 14.—*Dimensions of upper teeth of Artiodactyla sp. A,* Diacodexis gracilis, *and* Diacodexis minutus.

		P^3		P^4		M^1		M^2		M^3	
Specimen no.	Locality	L	W	L	W	L	W	L	W	L	W
				Artiodactyla sp. A							
UCM 47889	UCM 78049					3.7	4.4	4.2	5.7	3.4	5.5
UCM 48517	UCM 78049					3.6	4.8				
CM 43138	CM 941					3.9	5.0	4.1	5.6		
CM 43131	CM 941							4.5	6.0	4.1	6.3
UCM 47054	UCM 78049							3.7	5.4		
Mean						3.73	4.73	4.13	5.68	3.75	5.90
				Diacodexis gracilis							
UCM 52585	UCM 84256	4.8	2.5	3.6	4.0	3.6	4.2	3.9	4.8	3.5	4.4
				Diacodexis minutus							
CM 44913	CM 34	4.6	3.1								
CM 35786	CM 34					3.7	5.2				
CM 55139	CM 34					3.7	4.7				
CM 43712	CM 34					3.5	5.0				
UCM 44516	CM 34					3.2	4.7				
UCM 46808	UCM 81027					3.5	4.5				
UCM 44401	UCM 80062							4.0	5.0		
CM 35787	CM 34								5.5		
CM 35789	CM 34								5.9		
CM 36446	CM 34							3.9	5.0		
CM 37310	CM 34							3.6	5.2		
CM 55154	CM 34							3.7	5.1		
CM 36443	CM 34							3.9	5.3		
CM 43713	CM 34							4.0	5.1		
Mean						3.52	4.82	3.85	5.26		
N						5	5	6	8		

and compressed trigonid on M_{1-3}, and with metacone (weak) on P^4; additionally, differs from all species of *Diacodexis* (except *D. secans* lineage segment *D. s.-primus*) in lacking a postmetacristid and talonid notch on M_{1-3}.

Syntypic series and referred specimens.—UCM 52583–52585.

Localities.—UCM locs. 84180, 84250, 84255, 84256 (late Graybullian, Willwood Fm.), Bighorn Basin, Wyoming.

Known distribution.—Early Wasatchian (late Graybullian)—Bighorn Basin (Willwood Fm.), Wyoming.

Description.—Teeth anterior to P^3 and P_4 are unknown. P_4 is short and bears a double paraconid and a postmetacristid. Unlike M_1, the trigonid is compressed on M_{2-3} and the paraconid is severely reduced and more medial. Postmetacristids and talonid notches are absent and the metaconids are uninflated. P^3 is triangular in occlusal view, with a weak protocone offset posteriorly. P^{3-4} bear a weak metacone at the midpoint of the postparacrista, and a somewhat elongate, sharply pointed parastyle. M^{1-3} are uninflated, have sharp cusps, conules, and cristae, and perhaps the most distinct pseudohypocones among species of *Diacodexis*.

Discussion.—*D. gracilis* most closely resembles the *D. s.-metsiacus* lineage segment of *D. secans* in overall dental morphology, but is slightly smaller, has a more compressed trigonid and a more reduced and medial paraconid on M_{2-3}, and a slightly less inflated metaconid on M_{1-3}. It also differs from *D. minutus* in these features as well as in lacking a postmetacristid and talonid notch on M_{1-3}, and in having a much less inflated metaconid. Although there is no morphologic overlap between *D. gracilis* and these groups, some specimens of *D. s.-metsiacus, D. minutus,* and Artiodactyla sp. A approach the *D. gracilis* condition in isolated features. On a few molars of *D. minutus* (CM 21132, 22593, 37311, 37312) the paraconid is either nearly as weak or as medial as in *D. gracilis,* but the molars otherwise differ from the latter as described above. Similarly, the paraconid on some specimens of Artiodactyla sp. A is small, but never as reduced or as medial as in *D. gracilis.* The known material suggests that *D. gracilis* is most closely related to *D. s.-metsiacus* and independently evolved a reduced, more medial paraconid on M_{2-3} and a more compressed trigonid on M_{1-3}. It lacks the more derived character states of Artiodactyla sp. A and sp. B, *D. minutus, D. woltonensis,* and more evolved lineage segments of *D. secans.* Among known species of *Diacodexis, D. gracilis* exhibits the least amount of gradational difference from its putative ancestor. This may be due to small sample size (four specimens).

Artiodactyla sp. A (or spp.)

(Tables 1–2, 12, 14)

Diacodexis metsiacus, Kihm, 1984.

Referred specimens.—CM 43129–43132, 43134–43136, 43138; AMNH 16296—from the San Jose Fm. (late Graybullian–Lysitean), San Juan Basin, New Mexico. CM 10475, 43702; UCM 40831, 47052–47054, 47889, 47891, 48517, 48526—from the Debeque Fm. (late Graybullian–Lysitean), Piceance Basin, Colorado.

Discussion.—This small sample of artiodactyls from the San Juan and Piceance basins may represent one or two species of *Diacodexis* or a new genus. More material is needed for a systematic resolution of this sample. The lower molars have an uninflated metaconid, an elevated and conjoined paraconid and metaconid, a small paraconid anterior or barely anteromedial to the metaconid, an elongate talonid (most specimens), a broad postcingulid, and a lingual hypoconulid isolated from a conical entoconid, which is equal in height to the hypoconid in most specimens. The lower molars lack a postmetacristid and a talonid notch, but the talonid basin is open lingually due to the absence of a pre-entocristid. These features, in part, define the derived condition of antiacodontids and homacodontids and become further developed in these clades. The lower molars also lack the other specializations that define the most primitive known antiacodontid (*Antiacodon,* new species, Lostcabinian, Bighorn Basin), and homacodontid (*Hexacodus uintensis,* Lysitean–Lostcabinian, Wind River and Green River basins; Stucky and Krishtalka, manuscript).

P_3 is shorter than P_4. Both are gracile, lack a postmetacristid, and have a posterior trigonid wall that is concave, as in antiacodontids and homacodontids.

The upper molars are variable in the presence of a weak but distinct mesostylar flexure, which on CM 43138 (M^{1-2}) is formed by an extension of the premetacrista dorsally beyond the apex of the centrocrista to the ectocingulum. On M^3 (but not M^2) in CM 43131 and UCM 47889, the apex of the centrocrista has a slight labial flexure, which is not an extension of the premetacrista and does not reach the ectocingulum. The other upper molars in this sample (UCM 47054, M^2; UCM 48517, M^1) lack a mesostyle.

Both mesostylar conditions, as well as other mesostylar variations occur in homacodontids and antiacodontids. The second condition (on M^3 in CM 43131, UCM 47889) also occurs on two M^2s and all but one M^3 of *D. s.-kelleyi*; CM 43131 also resembles *D. s.-kelleyi* in the lingual distention of the periconal and hypoconal areas of the crown, and may represent the latter lineage segment of *D. secans* in the San Juan Basin. However, none of the lower molars in this sample is *D. s.-kelleyi*-like; the range of variation in the lower molars, as in the uppers, approaches the *D. s.-metsiacus* lineage segment of *D. secans* on the one hand, and antiacodontids and homacodontids on the other.

The lower premolars and some of the upper and lower molars in this sample from the San Juan and Piceance basins (CM 43129, 43135, 43138, 10475, 43132, 43134, 43136, 43130) seem more closely allied

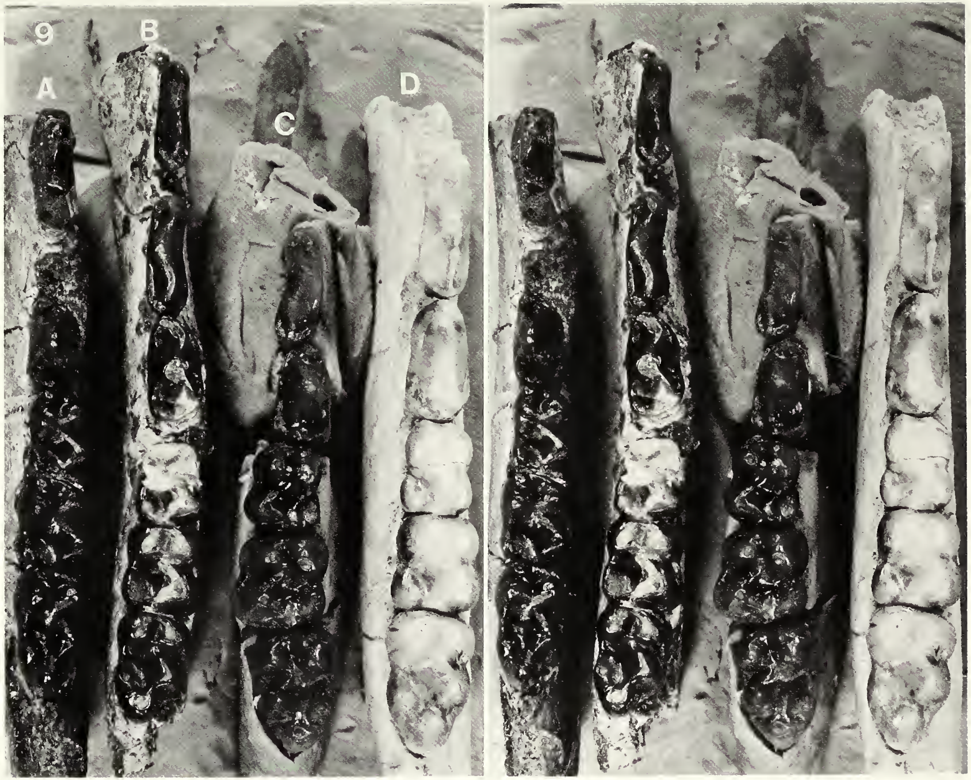


Fig. 9.—Chronoclinal shifts in morphology in the lower dentition of *Diacodexis secans* from the Sandcouleean to the Gardnerbuttean (A to D). (A) Lineage segment *D. s.-primus* (AMNH 15672); (B) lineage segment *D. s.-metsiacus* (AMNH 15666); (C) lineage segment *D. s.-kelleyi* (CM 39880); (D) lineage segment *D. s.-secans* (UCM 42199); all approx. ×2.

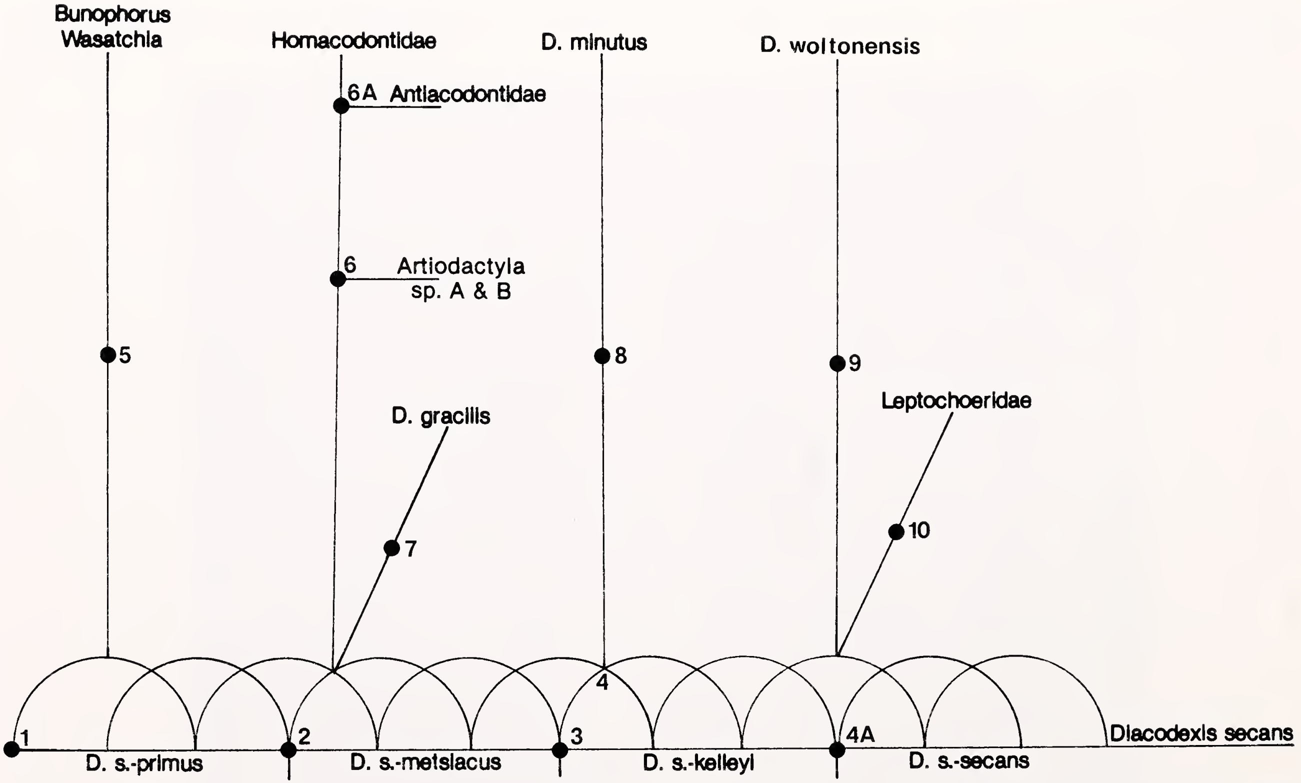


Fig. 10.—Phylogenetic relationships of *Diacodexis,* Artiodactyla sp. A, Artiodactyla sp. B, the *Wasatchia-Bunophorus* clade, Antiacodontidae, Homacodontidae, and Leptochoeridae. See text (conclusions) for an explanation of the derived characters at each node. Semicircles denote anagenetic change and overlap in the frequency and expression of derived features in *Diacodexis secans.*

with homacodontids and antiacodontids than any known species of *Diacodexis*. Other specimens in this sample (AMNH 16296; UCM 40831, 47052–47054, 47889, 47891, 48517, 48526) are also similar to most specimens of *D. s.-metsiacus*, in having a short, wide M_{2-3} talonid, a nearly square M_2, and slightly inflated cusps. All of the material referred here exhibits the elevated trigonid, the conical, high entoconid, the small anterolingual paraconid conjoined with the metaconid and the broad postcingulid that imply affinity with antiacodontids and homacodontids. All of these characters appear to be continuously variable within this group, which may represent one or two new and derived species of *Diacodexis* or a new genus, or, less likely, a geographic subspecies of *D. secans*. Whatever the systematic resolution, which awaits a larger sample from the southwestern basins, this group is morphologically intermediate between *D. secans* and the homacodontid-antiacodontid clade. The current record implies that the radiation of this clade began in the southern and western basins in the early Eocene.

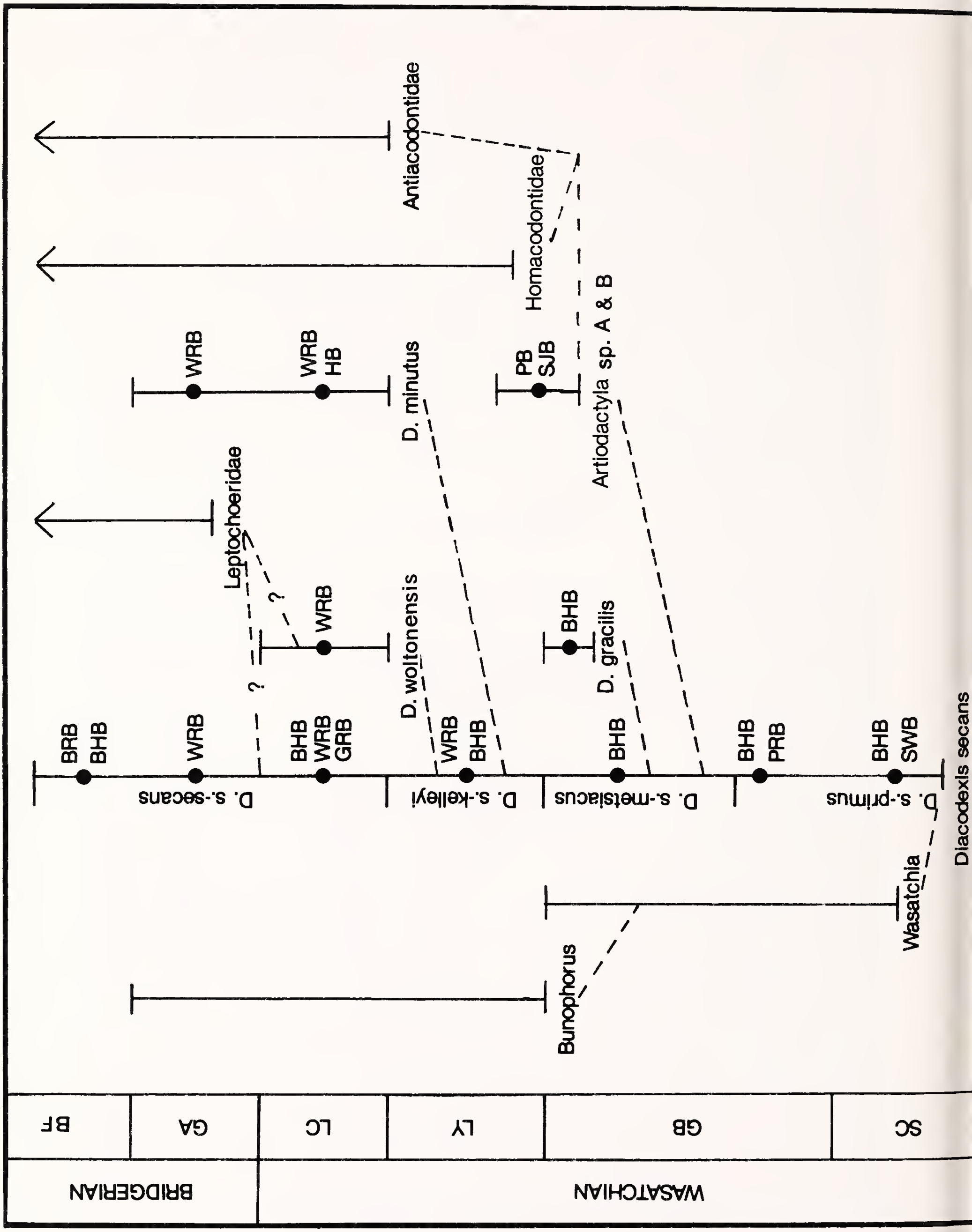
Artiodactyla sp. B
(Tables 1, 14)

Referred specimens.—CM 43128, 43133; AMNH 237, 86289—from the San Jose Fm. (late Graybullian–Lysitean), San Juan Basin, New Mexico.

These four specimens are larger, but otherwise virtually identical to Artiodactyla sp. A, especially those specimens that more closely resemble antiacodontids and homacodontids.

CONCLUSIONS

Three species of *Diacodexis* occur in the Wind River Formation in the northeastern and central parts of the Wind River Basin—*D. secans*, *D. minutus* and *D. woltonensis*. *D. secans* includes as synonyms *D. metsiacus*, *D. brachystomus*, *D. laticuneus*, and *D. olseni*, and also occurs in the Bighorn, Green River, and Powder River basins, Wyoming, and the Sand Wash Basin (Four Mile area), Colorado. *D. secans* is known from Sandcouleean (earliest Wasatchian) through Blacksforkian (middle Bridgerian) horizons, and is divided into four, informal, temporally successive lineage segments (*D. s.-primus*, *D. s.-metsiacus*, *D. s.-kelleyi*, *D. s.-secans*) to reflect stages in its anagenetic evolutionary history (Figs. 9–11). In the Wind River Basin *D. secans* is represented by *D. s.-kelleyi* in the Lysite Member (Lysitean) and *D. s.-secans* in the Lost Cabin Member (Lostcabinian-Gardnerbuttean). *D. minutus* and *D. woltonensis* are new species; both co-occur with *D. secans* in the Lostcabinian, as does the former in the Gardnerbuttean (Figs. 12, 13). Other diacodexeines and allied taxa discussed here are unknown


BRIDGERIAN
WASATCHIAN
BF
GA
LC
LY
GB
SC
Diacodexis secans
D. s.-primus
BHB SWB
BHB PRB
D. s.-metsiacus
BHB
D. s.-kelleyi
WRB BHB
D. s.-secans
BHB WRB GRB
WRB
BRB BHB
Wasatchia
Bunophorus
D. gracilis
BHB
Artiodactyla sp. A & B
PB SJB
D. woltonensis
WRB
D. minutus
WRB HB
WRB
Leptochoeridae
?
?
Homacodontidae
Antiacodontidae

from the Wind River Basin—*D. gracilis,* new species, from the late Graybullian of the Bighorn Basin; and Artiodactyla sp. A and sp. B, from the middle Wasatchian of the Piceance and San Juan basins. Recognition of all of these species is based primarily on non-meristic morphological features and, in certain instances, on differences in size.

D. secans is the main species-lineage of diacodexeines and appears to have been ancestral at different points in its anagenetic history to all other species of *Diacodexis,* as well as Artiodactyla sp. A and sp. B, the *Wasatchia-Bunophorus* clade, homacodontids, antiacodontids, and leptochoerids. Evolution within *D. secans* involved the chronoclinal increase in degree and frequency of expression of a number of derived morphological features (see diagnosis of each lineage segment and pp. 421–422 for summary). Morphoclinal evolution and canalization of derived traits also characterized the cladogenetic appearance of *D. woltonensis, D. minutus,* and Artiodactyla sp. A. Depiction of such morphoclinal continua in a cladogram of strictly dichotomous relationships based on derived, digital character states is not possible. We present a cladogram-like figure (Fig. 10) as a synopsis of diacodexeine relationships, with the following warnings: (1) It is not dichotomous. (2) Most of the nodes involve derived morphoclinal characters rather than digital ones; also, the species and lineage segments exhibit internal and continuous variation; thus, not every specimen assigned to a species or lineage segment bears every derived character at that node to the same degree. (3) Sister species approach and, in some instances, show partial morphologic overlap with one another in derived features, which, in our opinion, reflects the real and fuzzy boundaries between some species, given an adequate fossil record. This reconstruction of relationships among diacodexeines and allied taxa is based both on the determination and integrity of species in the fossil record, and the pattern of shared-derived morphological features among them. Besides the well-known phylogenetic principles of plesiomorphy and apomorphy, application of the too oft forgotten principle of "variamorphy," or variation, is also required.

D. secans lineage segment *D. s.-primus* (Fig. 10, node 1) represents the primitive condition, from which the *Wasatchia-Bunophorus* clade

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←

Fig. 11.—Phylogenetic relationships and known occurrence (diagramatic) of the species of *Diacodexis,* Artiodactyla sp. A, and Artiodactyla sp. B. Abbreviations are: Land Mammal Sub-ages—SC, Sandcouleean; GB, Graybullian; LY, Lysitean; LC, Lostcabinian; GA, Gardnerbuttean; BF, Blacksforkian. Basins—BHB, Bighorn Basin; BRB, Bridger Basin; GRB, Green River Basin; HB, Huerfano Basin; PB, Piceance Basin; PRB, Powder River Basin; SJB, San Juan Basin; SWB, Sand Wash Basin; WRB, Wind River Basin.

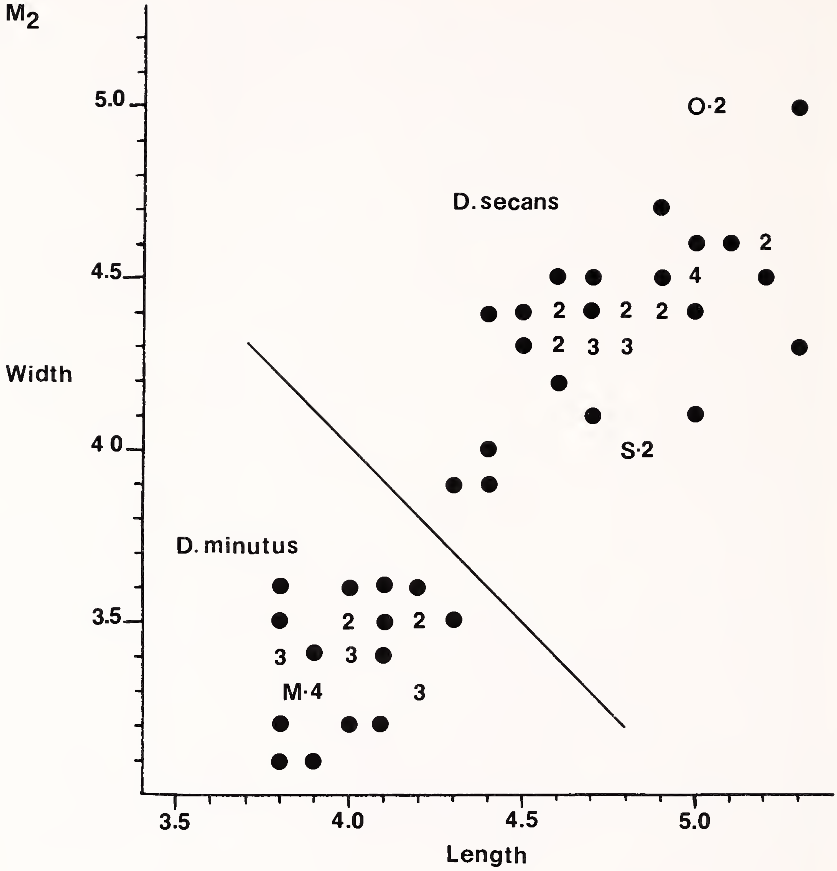

Fig. 12.—Plot of length and width of M_2s of *D. secans* and *D. minutus* from a single horizon at CM loc. 34 (Gardnerbuttean). S, holotype of *D. secans* (from AMNH loc. Wind River beds); O, holotype of *D. olseni* (CM loc. 34); M, holotype of *D. minutus* (CM loc. 34). Numbers indicate number of specimens of that size.

is derived (node 5) in larger size, greater robusticity and bunodonty, and reduction of P_4 paraconid. The latter clade retains the primitve condition in lacking a postmetacristid on P_4–M_3, a talonid notch on M_{1-3} and, initially (*Wasatchia*), in having an unreduced molar paraconid directly anterior to the metaconid. The derived condition (postmetacristid on P_4–M_3; talonid notch on M_{1-3}, with paraconid reduced and slightly medial) defines most specimens of *D. s.-metsiacus* (node 2), some of which also approach the derived morphology of Artiodactyla sp. A and sp. B (node 6)—elevated and conjoined paraconid

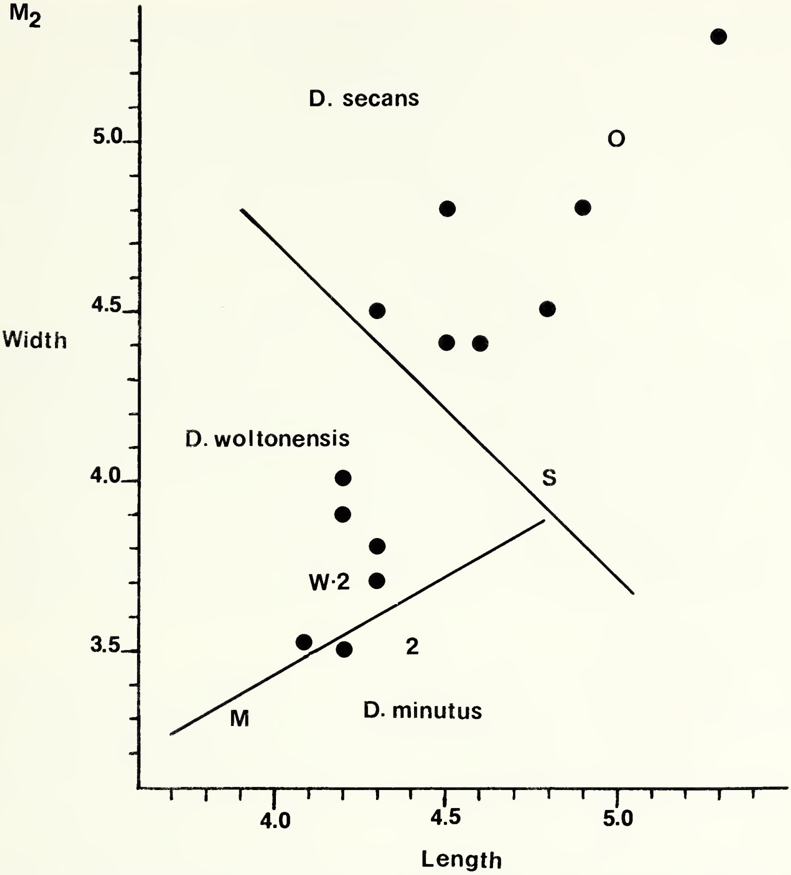

Fig. 13.—Plot of length and width of M_2s of *D. secans, D. minutus,* and *D. woltonensis* from Lostcabinian localities in the Wind River Basin. S, holotype of *D. secans* (from AMNH loc. Wind River beds); O, holotype of *D. olseni* (CM loc. 34, Gardnerbuttean); M, holotype of *D. minutus* (CM loc. 34, Gardnerbuttean); W, holotype of *D. woltonensis* (CM loc. 1077, Lostcabinian). Numbers indicate number of specimens of that size.

and metaconid; hypoconulid lingual, close to, but isolated from a tall entoconid, which is subequal to the hypoconid; broad postcingulid; talonid open lingually between bases of metaconid and entoconid. These features are retained and further modified in primitive antiacodontids and homacodontids (node 6A; Stucky and Krishtalka, manuscript). Also derived over the *D. s.-metsiacus* condition is *D. gracilis* (node 7), in its severely reduced and more medial paraconid on M_{2-3}, compressed trigonid on M_{1-3}, small size and more gracile cusps. *D. s.-kelleyi* and all other diacodexeines and leptochoerids (node 3) are derived over *D. s.-metsiacus* in the greater frequency and degree of expression of an expanded molar metaconid, hypoconid and protocone, a molar talonid notch, a P_4 and molar postmetacristid, elongate $P^3/_3$, stronger P^3 protocone, and shorter M_3 hypoconulid lobe. *D. minutus, D. woltonensis* and *D. s.-secans* (node 4) share the most frequent presence and strongest development of a molar talonid notch and P_4–M_3 postmetacristid, but, as discussed above, these features may have arisen in parallel in *D. minutus* and these taxa from *D. s.-metsiacus. D. minutus* is derived (node 8) in its deeper talonid basin, small size, and concomitant more distinct conules, conulecristae and less inflated cusps. *D. woltonensis* and *D. s.-secans* (node 4A) are most robust, and differ from one another principally in size, with the former being most robust in proportion to its smaller size (node 9), and having a shallower talonid basin. Leptochoerids (node 10) share the major features and robusticity of *D. s.-secans* and *D. woltonensis,* but are further derived in the hypertrophy of $P^4/_4$ and $M^1/_1$, the progressive decrease in size of the molars from $M^1/_1$ to $M^3/_3$, and the deeper talonid basin on M_{1-2}.

These relationships, along with the known occurrence of the taxa, are depicted in a temporal framework in Fig. 11. The polarities of the shared-derived features among these taxa coincide with their stratigraphic occurrence.

The fossil record of North American artiodactyls, like that of primates, perissodactyls, rodents, insectivores, and some condylarths, is sufficiently rich and dense to reveal evolutionary tempo and mode. A measure of the latter is the kind and degree of morphological difference between sister species combined with the stratigraphic record. The particular circularity discussed in the introduction—where species determinations result *a priori* in certain evolutionary patterns and vice versa—has, we think, been avoided. The diacodexeine species recognized here are grounded in morphological distinction among lithosympatric and/or penecontemporaneous units. The evolutionary patterns emerge independently from the congruence of shared-derived features and their polarities among these species in a stratigraphic context.

Among the diacodexeines and allies treated here, the evolutionary tempo appears to have been gradual, with chronoclinal shifts in the degree and frequency of expression of evolving features, and their canalization within single lineages and branching taxa. As a corollary, morphologic change within these artiodactyls is mosaic—rates, patterns, and amount of change of individual features vary from incrementally continuous and slow (for example, the development of a postmetacristid and talonid notch on the lower molars of *D. secans*), to more nearly abrupt (for example, the appearance of a severely reduced and nearly medial paraconid on M_{2-3} of *D. gracilis*), to stasis (for example, fixation of a slightly internal molar paraconid in three lineage segments of *D. secans*). The degree of gradualism appears to be greater in lineage-species (for example, *D. secans*) and less at cladogenetic events (for example, the origins of *D. woltonensis* and *D. minutus*); the apparent difference in rates will be tested by a more dense fossil record. Microevolutionary processes can account for both cladogenesis and anagenetic change among these artiodactyls; macroevolutionary processes are not called for.

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NOTES ADDED IN PROOF.—1. In Table 7 (p. 450), the sequence of specimens UCM 52551B–52551L, 52556B, 52562B has been renumbered as UCM 52586–52598, respectively.

2. Since this paper went to press, two critical articles concerning *Diacodexis* have appeared. K. D. Rose (J. Paleont., 59:1203–1226, 1985) now holds that the postcranial specializations in *Diacodexis* may not preclude its basal position within Artiodactyla, a conclusion corroborated by the dental evidence presented in this paper.

P. D. Gingerich (Paleobiol., 11:27–41, 1985) contends that early Wasatchian *Diacodexis metsiacus* (=*D. secans* of this paper) exhibits evolutionary stasis, in contrast to the evidence presented here for significant morphologic anagenesis in this Wasatchian (54.5 ma)-early Bridgerian (50 ma) species-lineage. This contrast, and Gingerich's apparent stasis in *D. secans,* applies only to the log L × W of M_1. Size of M_1 is indeed static, as we note several times in this paper. However, the log L × W of M_1 is neither the sole morphology of *D. secans,* nor the sole indicator of evolutionary tempo. As discussed above, suites of other dental characters in *D. secans* show moderate to considerable anagenetic change.

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YANOMAMA MATERIAL CULTURE IN THE CARNEGIE MUSEUM OF NATURAL HISTORY. PART I. FOOD PROCUREMENT AND HOUSEHOLD ARTICLES

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Abstract

The Carnegie Museum of Natural History has one of the largest, most inclusive, and best documented collections of Yanomama material culture in the world. The collection, consisting of two accessions comprising 572 specimens, spans a 5 year period from 1979 to 1984. This corpus of material documents not only traditional Yanomama material culture, but also shows the changes it has undergone due to the introduction of Western goods and materials. Part I deals with material culture categories related to Food Procurement and Household Articles. Wearing Apparel and Festival Artifacts, and Foreign Influence and Miscellaneous Constructions will be published as Parts II and III, respectively.

Introduction

The Yanomama Indians inhabit an area of approximately 30,000 (Smole, 1976:3) to 100,000 (Migliazza, 1972:20) square miles in northern Brazil and southern Venezuela (Fig. 1). They are one of the largest unacculturated Indian populations in the Amazonian rain forest, remaining isolated until the present due to their settlement locations away from major waterways in the Guyana Shield area. There is no agreement on the total number of Yanomama. While Chagnon (1974: 1) estimates a total population of 10,000, Saffirio (1985:36) feels that 16,400 in 320 villages is closer to the true number.

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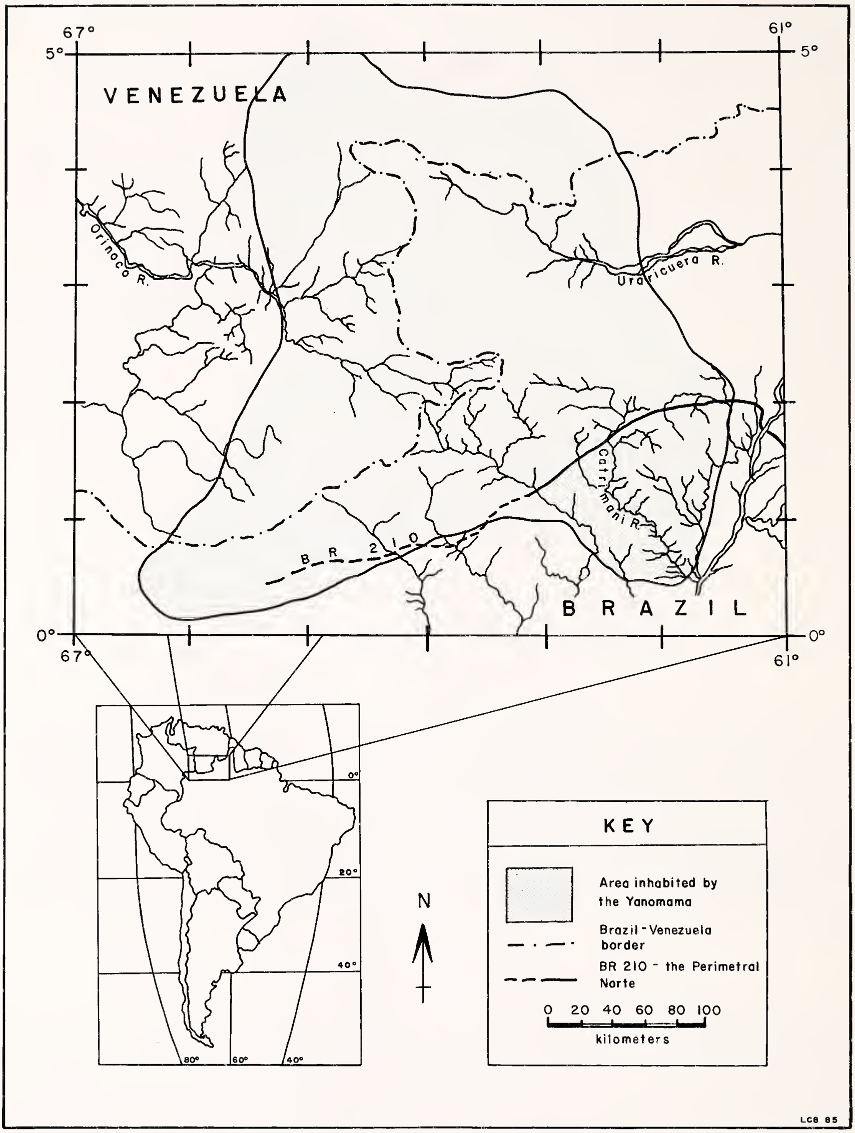

Fig. 1.—Area occupied by the Yanomama Indians in northern Brazil and southern Venezuela.

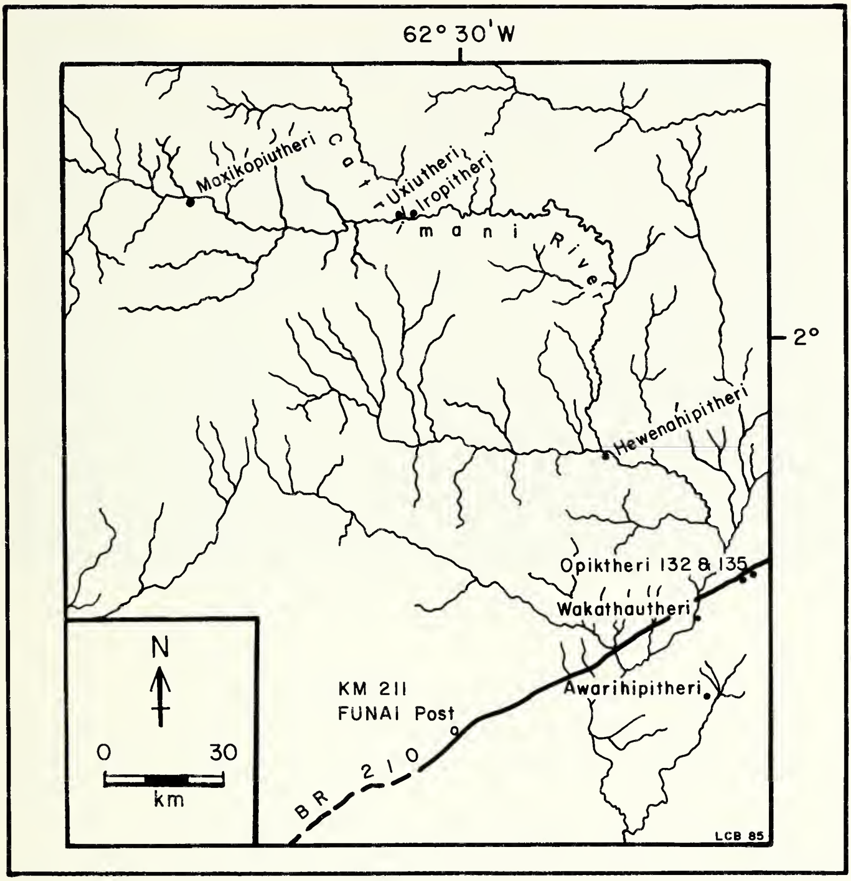

Fig. 2.—The Catrimani River Yanomama area and villages.

All Yanomama speak four mutually intelligible languages and several dialects. They distinguish themselves from other Indians by language and between groups of Yanomama by dialect. The group has been called by several names; terms such as "Waica," "Xiriana," "Shamatari," and "Yanoama," have all been used to designate this family of languages. "Yanomamo," "Yanam," "Sanuma," and "Yanomam" actually denote only one dialect or language within the larger group. "Yanomama" is used to refer to the entire family of languages (Migliazza, 1972:33).

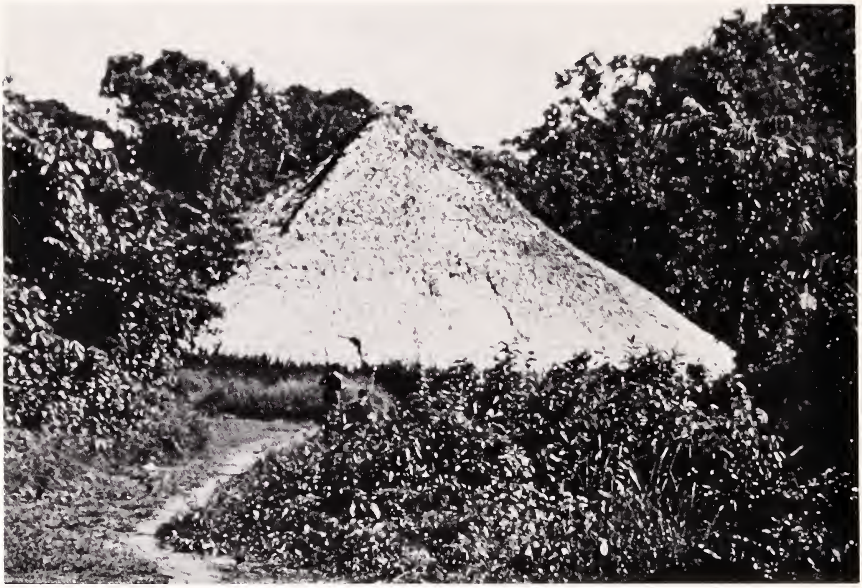

Fig. 3.—A village in the Catrimani River area.

CATRIMANI RIVER YANOMAMA

The Catrimani River Yanomama of Brazil (Fig. 2), from whom the Carnegie Museum of Natural History collections have come, belong to the linguistic group "Yanomam." They inhabit areas of the Federal Territory of Roraima and the State of Amazonas. Each village usually consists of one communal house from 60 to 120 ft in diameter (Fig. 3). The most common structure is round with one or two small smoke holes in the top. The house, always built near the gardens and a stream, is constructed entirely of forest materials. Five to 20 families, interrelated by marriage, each build and occupy the section of the house assigned to it by kinship rules. Total village population ranges from 15 to 80 people, with an average number of 35.

The Yanomama spend almost as much time gathering and hunting as they do gardening, but the latter is more rewarding in terms of total calories produced (Saffirio, 1980:26). While men clear and plant the garden, harvesting is the domain of the women. Hunting is strictly a male occupation. A 15-km radius of forest, approximately a 3½ hr walk from the village, is exploited in gathering and hunting. Peach palms and several varieties of bananas are harvested for years in old abandoned gardens (Saffirio, 1980:27)

FOREIGN INFLUENCES

The Yanomama were largely unknown to the Western world until the 1950's. But since the construction in the mid-1970's of Brazilian Highway BR-210, the Perimetral Norte, deep into Yanomama territory in Brazil, acculturation has been proceeding at a rapid rate (Migliazza, 1978:17; Ramos,1979). The introduction of Western goods, beliefs, and diseases has brought about profound and permanent changes in the Yanomama lifestyle (Lizot, 1976; Saffirio et al., 1983). Like many indigenous South American groups before them, the Yanomama are substituting Western material culture in place of their traditional technology. This loss of native crafts is documented in the Carnegie Museum of Natural History collections.

Among the Catrimani River Yanomama, sustained contact with Westerners began in 1965 when two Catholic missionaries from the Consolata Society for Foreign Missions settled permanently on the mid-Catrimani River. After building a few houses and a medical dispensary, they expanded contact to all nine Yanomama villages in the Catrimani River basin. In 1974 the Perimetral Norte, BR-210, reached the Catrimani River. Hundreds of highway workers entered the area, bringing flu and measles with them. These diseases, as lethal to the Yanomama as they were to many native North American groups in the 19th and early 20th centuries, caused drastic decreases in population. In some villages, the death toll reached 51%. A vaccination program for the Yanomama, run by the Brazilian Indian Agency (FUNAI) and the Consolata Missionaries, has succeeded in reaching almost all of the Yanomama around the Catrimani River and stemming the worst of the tide.

Goods introduced between 1965 and 1974 were limited in amount as well as in diversity. These early acquisitions consisted mainly of machetes, fish hooks and lines, beads, matches, and salt. Western goods became abundant and varied after the penetration of Highway BR-210 into Yanomama territory, accessible through highway workers, miners, and settlers. In the eyes of the Yanomama, Brazilian society is superior for its material goods and its technical power. Given the choice between the same Brazilian and Yanomama products, both of them well-made and convenient, Yanomama generally select the Western product (Saffirio, 1980:39). Clay pots for cooking, cumbersome and fragile, are being replaced by aluminum pots. Some Yanomama have also substituted metal sheets for their clay cassava griddles. Brazilian hammocks are taking the place of homemade Yanomama hammocks. Western clothes, especially in villages located on Highway BR-210, have made traditional women's aprons obsolete, and the men no longer tie their penis foreskin to a waistcord. Seed necklaces, traditionally made

Table 1.—*Cordage types used by Yanomama.*

Number	Cordage type	Cordage notation
1	single ply S twist *yamaasik* fiber	S
2	single ply Z twist *yamaasik* fiber	Z
3	two ply s spin Z twist *yamaasik* fiber	s Z s
4	two ply z spin S twist *yamaasik* fiber	z S z
5	variable number of s spin *yamaasik* fibers, final Z twist	Z s
6	variable number of 2 ply s spin Z plied *yamaasik* fibers, final S twist	s S z s
7	single ply S twist cotton	S
8	single ply Z twist cotton	Z
9	two ply s spin Z twist cotton	s Z s
10	two ply z spin S twist cotton	z S z
11	variable number of s spin cotton fibers, final Z twist	Z s
12	variable number of z spin cotton fibers, final S twist	S z
13	variable number of two ply s spin Z plied cotton yarns, final S twist	s S z s
14	variable number of three ply s spin Z plied cotton yarns, final S twist	s S z s s
15	variable number of two ply z spin S plied cotton yarns, final Z twist	z Z s z
16	two ply s spin Z plied cotton, final Z twist	z s s Z z s s

Table 1.—*Continued.*

Number	Cordage type	Cordage notation
17	two ply s spin Z plied cotton, final Z twist	s z s s Z s z s s
18	two ply z spin S plied cotton, final S twist	s z z S s z z
19	two ply s spin Z plied S plied cotton, final Z twist	z s s s z s s Z z s s s z s s
20	two ply s spin Z plied S plied cotton, final Z twist	z s s s z s s z s s Z z s s s z s s z s

by Yanomama women, are rarely made as trade beads are popular and widely available.

THE COLLECTION

Giovanni Saffirio, a member of the Consolata Society for Foreign Missions, lived as a Catholic missionary near a Yanomama village on the mid-Catrimani River from October 1968 to August 1977. For two years, from October 1977 to October 1979, he studied anthropology at the University of Pittsburgh in Pennsylvania. Returning to the Yanomama in October 1979, he spent five additional months on the Ca-

Table 2.—*Knot types used by Yanomama.*

Letter	Knot	Letter	Knot
A	simple overhand	F	square knot
B	figure of eight with the bow passing through the bight	G	granny knot
		H	lark's head
		I	simple overhand noose with a half hitch
C	simple overhand noose		
D	clove hitch	J	half hitch
E	simple overhand with a half hitch	K	half hitch noose
		L	wrap

trimani River doing research for his Master's degree, awarded in 1980. He has recently been awarded his Ph.D. in the Department of Anthropology at the University of Pittsburgh, and has since returned to the Catrimani Mission.

Collection I, accession number 32703, was made during 1979–80, while collection II, accession number 32735, was acquired in 1984. Every effort was made to secure as complete a representation of Yanomama material culture as possible, with a wide range in variation among specimens. As a result, the Carnegie Museum of Natural History has one of the largest, best documented, and most inclusive collections in the world.

The total number of specimens in both collections I and II is 572 objects. Toys as well as weapons were obtained. Hunting equippage is extensive; however, machetes or hoes for gardening are lacking as these are not made by the Yanomama. Clay cooking pots, spindles and balls of cotton, and gourd cups and spoons are all present. Implements used during feasts or shamanistic ceremonies are also represented.

It proved impossible to fully explain all manufacturing terminology and methods of the many different materials (basketry, cordage, knots) used in construction of the specimens. Standard references were used—Emery (1980) when discussing the cordage, Adovasio (1977) for the basketry, and Shaw (1972) for knot descriptions.

Knots and cordage have been tabulated, and numbers for the cordage and letters for the knots will be used throughout the analysis (see Tables 1 and 2). All knots are illustrated (Fig. 4). "S" and "Z" twist in cordage is also illustrated (Fig. 5).

Some of the cordage consists of a number of spun and plied yarns which were combined by twisting. Rather than list these varying numbers of yarns in the final products as separate constructions, they were combined in one cordage type in Table 1, with the number of plied yarns referred to in parentheses after the cordage type number. For example, cordage type #12(4) consists of four pieces of 2 ply s spin Z twist yarns, all combined in an S twist. Similarly, cordage type #13(4)

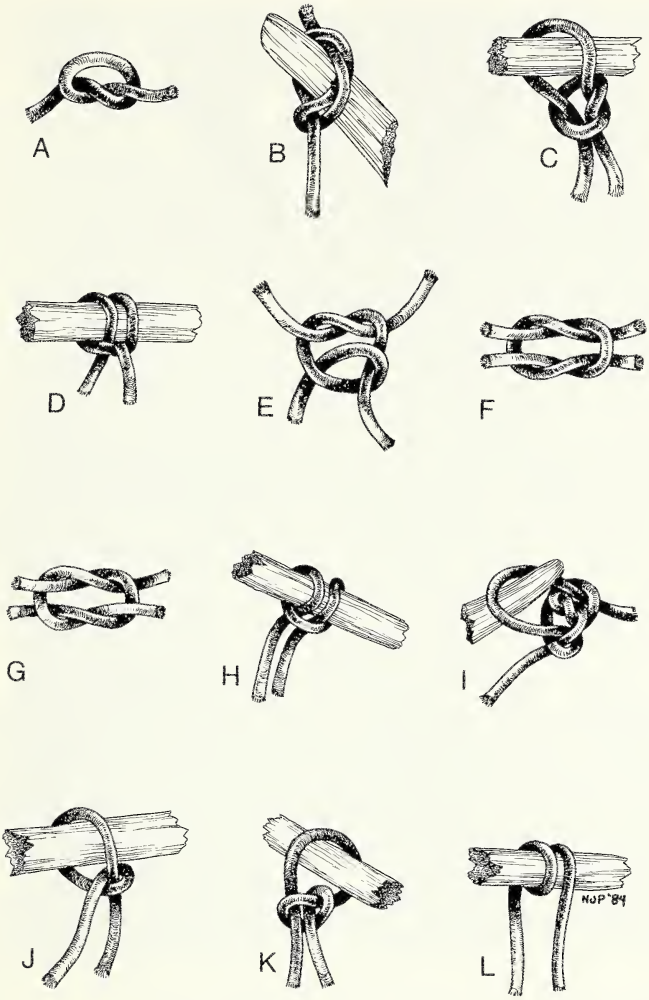

Fig. 4.—Knots used by the Yanomama (see Table 2) in specimen manufacture.

is composed of four pieces of 3 ply s spin Z twist yarns, combined in an S twist. Cordage types #5 and #6, as well as #11 through #15, all consist of varying numbers of plies, and will be used with parenthetical numbers indicative of these.

All Yanomama words in the text are set in italics. Their spelling follows Saffirio (1980, 1985). Due to the great number of Yanomama languages and dialects, these words are specific to the Catrimani River villages only.

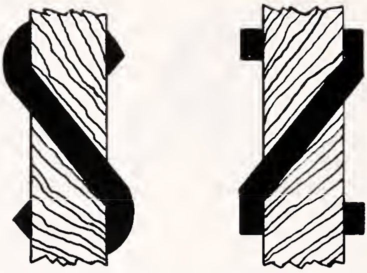

Fig. 5.—S and Z twist in cordage (after Emery, 1980).

FOOD PROCUREMENT

The Yanomama are horticulturalists, hunters, and gatherers. Garden crops such as the plantain, *Musa* sp., provide the major portion of the diet. Hunting, fishing, and collecting provide necessary proteins and fats not found in cultivated plants. The Carnegie Museum of Natural History collection contains hunting and fishing equippage, but no tools for collecting or gardening. The gardening equipment is very limited; machetes, axes, hoes, and digging sticks.

Hunting Implements

Hunting is an exclusively male activity, and excellence in hunting is the primary way for a young male to increase his status within a village. As a result, younger Yanomama men spend more time hunting than gardening; every day an individual or a small kin group makes a hunting trip lasting from 3 hrs up to an entire day. Hunting parties made up of the entire village and lasting a week or more are less frequent, often taking place before a festival. The Catrimani River Yanomama do not use the blow gun and poisoned dart common to some other Yanomama groups, but rely instead on the bow and arrow (Fig. 6). Each hunter carries a bow, three to five arrows, and a bamboo case or quiver which holds extra arrow points and tools to sharpen them.

*Bows (*nahi*).*—The bow is fashioned from one of four types of young palm wood. The bow for an adult male ranges from 150 to 215 cm in length and is approximately 4 cm thick, while that for a boy will measure up to 90 cm long and 1.5 cm thick. Boys begin to play with bows and arrows around the age of four, and go on their first real hunt at about 16.

Bow wood is collected in the forest and taken to the house to be reduced in size and roughly shaped with a machete. The lower jaw of a peccary is then used like a plane to smooth and shape the surface.

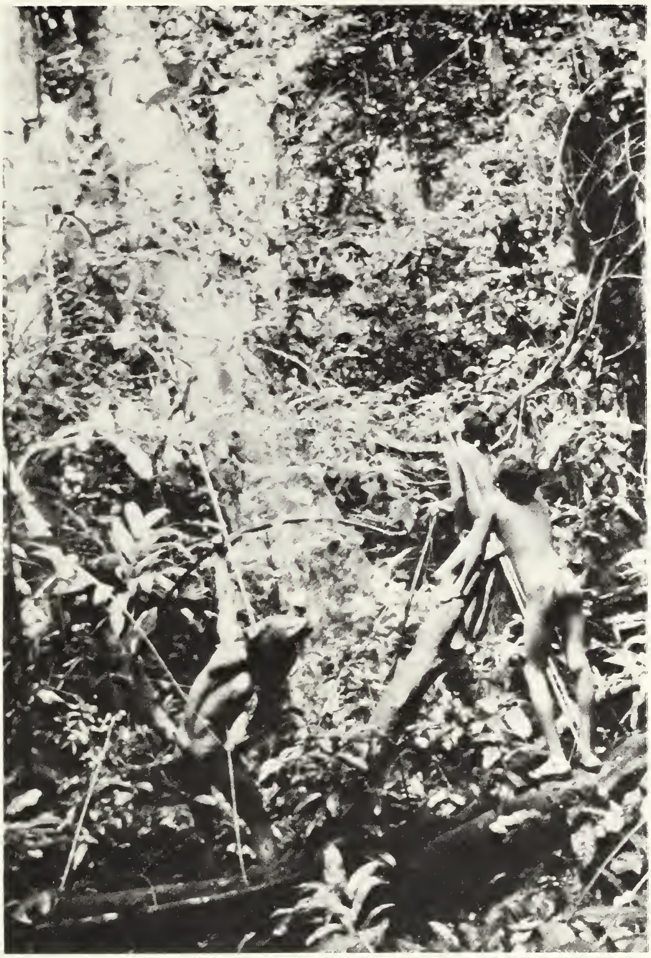

Fig. 6.—Yanomama hunting monkeys in the forest.

In cross-section, the bow forms a semi-circle with the flat part facing the hunter.

Bows are strung with strongly twisted *yamaasik* (*Annas parguasense camango*) fibers which are then waxed to keep them from splitting and rotting. The string is tied to the bow at each end (Fig. 7) and one end is usually clipped short. The other has a length of fiber (3 to 15 cm) left dangling in order to tighten or loosen the string as needed. This length of string is usually knotted on the end to keep it from unravelling.

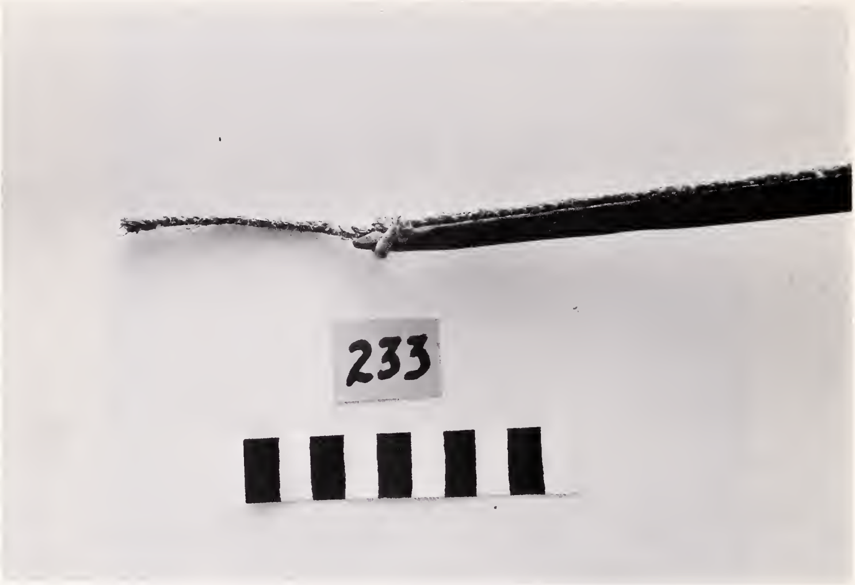

Fig. 7.—Detail of bow string attachment to the bow using knot "B." Accession #32735.

In the analysis, these will be referred to as the "clipped end," the "dangling end," and the "string ends," respectively.

Several facts are apparent from Table 3. On over 75% of the bows, at least one string end is finished off with a knot (type "A") to keep it from unravelling. The most common knot for attaching the string to the bow is type "B," the figure of eight with the bow passing through the bight. The second most popular knot, type "A," is used on only 3 bows and the third, type "D," on only 2. Clearly there has been no change in knot technology in the 4-year span between collections.

This is, however, not true in the cordage technology. In the earlier collection, all of the bows except 32703-34 and -79 have three or four ply cordage. In the later 32735 collection, none of the cordage has more than two plies. The average bow length has also decreased. In collection I the mean length is 196.98 cm, while collection II averages only 152.73 cm. The explanation for this lies in the fact that most of the collection II bows were made for young men and children who are not able to handle the long adult equipment.

The only other bows present in the CMNH collection are two unfinished bows, roughly shaped and unstrung:

Table 3.—*Bows of the Yanomama.*

Cordage type	String end knots	Clipped end knots	Dangling end knots	Bow length (cm)	Accession number
#3	none	B	B	216.0	32703-34
	A (1)*	B	B	221.0	-79
	A (1)	B	B	123.0	32735-227
	A (2)	A	D	156.2	-228
	A (1)	B	B	168.0	-229
	A (1)	B	B	172.4	-230
	none	B	B	156.5	-231
	A (1)	B	B	135.0	-232
	A (1)	A	B	158.0	-233
#5 (3)	none	B	B	216.0	32703-72
	none	B	B	193.7	-73
	A (1)	B	B	172.0	-74
	A (1)	B	B	140.0	-75
	none	B	B	180.0	-76
	A (1)	B	B	155.0	-77
	A (1)	B	B	202.0	-78
	A (1)	B	D	212.0	-80
	A (2)	B	B	189.0	-81
#5 (4)	A (1)	B	B	216.1	32703-71
#16	A (1)	B	B	218.0	32703-82
	A (1)	A	B	227.0	-83

* The number in parentheses refers to how many of the string ends are tied.

32735-234, unfinished bow of unknown palm wood; unstrung, with one end pointed and the other flat; L—160.3 cm.

32735-235, same as 32735-234; L—159.6 cm.

*Arrows (*xaraka*).*—Arrows propelled by the bows have a maximum horizontal range of 20 to 25 m and a maximum vertical range of about 30 m. Arrows in the collection average 175.0 cm in length. The shafts are fashioned from cultivated cane (*Gynerium sagittatum*) grown in the garden and dried in the sun or over a fire. Split curassow or bush turkey (Cracidae) feathers are bound to one end with *yamaasik* string or cotton to make the arrow spin in flight (Fig. 8). Four types of arrows are manufactured, differentiated by the kind of point attached to the shaft. Carnegie Museum of Natural History has three of the types in its collection (Fig. 9)—the barbed points used to hunt fish and birds, the pencil-like palm points used to hunt monkeys, and the lanceolate big game points. The fourth type, made on the spot from a knotted branch, is used to stun birds without damaging the plumage. The feathers are then used to manufacture earrings, armbands, and necklaces.

In the case of the barbed fish and bird arrows and the monkey arrows,

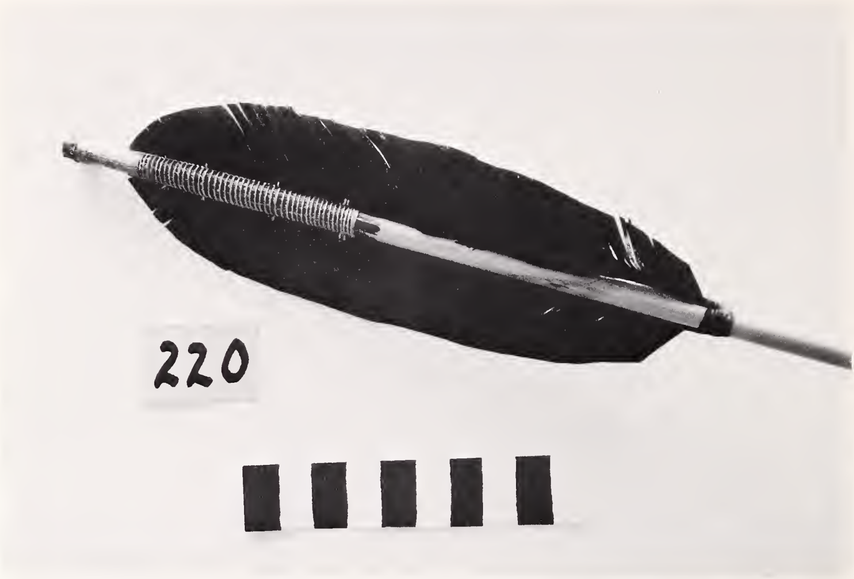

Fig. 8.—Arrow fletching, with cordage type #9 on the upper (nocked) end and cordage type #1 on the lower (point) end. Accession #32735.

the shaft end into which the point is inserted is narrowed. This ensures that the shaft will closely approximate the width of the point. The points are then jammed into the cane shaft, occasionally splitting the end. This is then wrapped with some type of cordage to hold the point firmly in place.

Single barbed-point arrows (*xaraka* with *atarihi* point) are used to shoot fish and birds. The barb, fashioned from a monkey bone lashed to a pointed stick, holds fast as the game tries to flee.

As can be noted in Table 4, the differences between the 19 arrows in collections I and II are striking. While the average arrow length for accession 32703 is 207.81 cm, that for accession 32735 is only 149.61 cm. The points have also decreased in length; the average for 32703 is 20.14 cm and that for 32735 is 12.59 cm. Again, arrows in the 32735 collection belonged to juveniles and children, causing them to be shorter than the 32703 collection.

The preferred point lashing material in both collection I and II is clearly cordage type #1, the single ply S twist *yamaasik* fiber. Only one arrow, 32703-92, uses the single ply Z twist *yamaasik* fiber, cordage type #2. This Z twist fiber is unusual; nearly all of the single ply fiber

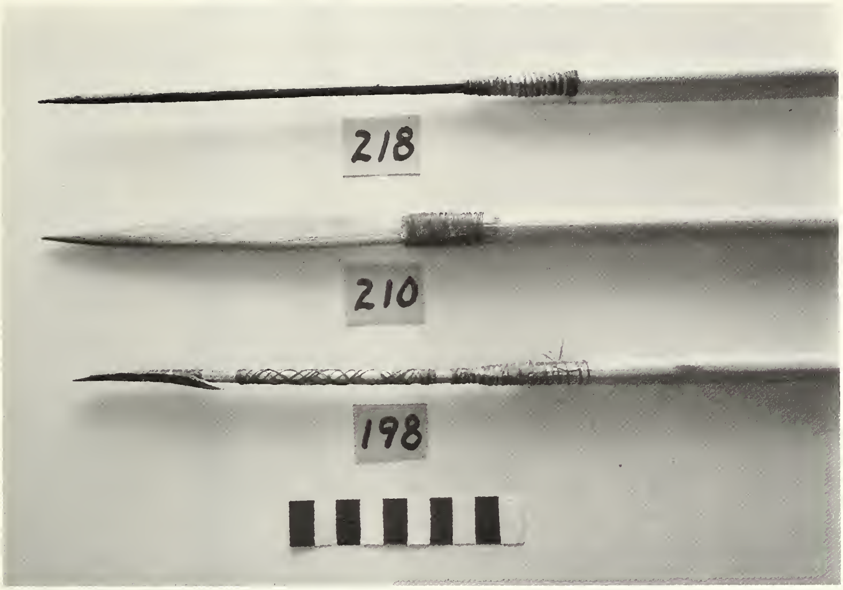

Fig. 9.—The three types of Yanomama arrow points from the Carnegie Museum of Natural History collection. From top: monkey point, big game point, and fish and bird point. Accession #32735.

on all artifacts in both collection I and II, as well as the initial spin on the multi-ply fiber cordage, is S twist.

Cordage type #9 is the favorite medium to wrap the upper end of the feathers. It is used on 90% of the accession 32703 arrows, and on 78% of the 32735 arrows.

The lower end feather wrapping is almost evenly divided between *yamaasik* fiber and cotton; the fiber wrapping is used on 10 arrows while the cotton cordage is present on nine. As on the upper end feather wrapping, cordage type #9 is slightly less popular on the lower end of the feathers in collection II; 323703 uses it 56% of the time while 32735 uses it only 40%.

Arrows with pencil-like points of palm wood (*xaraka* with *raxasi* point) are usually coated with poison and used in monkey and sloth hunting. The poison relaxes the grip of the animal, causing it to fall to the ground rather than remain locked in a death grip to the tree. The point is usually grooved near the shaft attachment, causing it to break off in the animal. This ensures that enough poison will enter the animal's bloodstream to be effective. In addition, the shaft will then fall

Table 4.—*Fish and bird arrows of the Yanomama.*

Accession number	Point wrapping	Feather wrapping		Length (cm)	
		Upper*	Lower	Arrow	Point
32703-33b	1	9	9	219.5	16.9
32703-91	1, 3†	9	9	217.7	22.5
32703-92	2	9	2	209.6	26.0
32703-95	1	1	1	195.1	16.9
32703-96	1	1	1	215.8	21.0
32703-97	1	9	9	226.7	24.3
32703-98	1	9	9	196.0	18.5
32703-99	1, 3†	9	1	216.6	15.0
32703-100	1‡	9	9	173.3	
32735-198	1	1	1	136.2	7.1
32735-199	1	9	9	165.4	6.3
32735-219	1	9	9	150.2	17.3
32735-220	1	9	1	158.8	9.8
32735-221	1	9	1	149.3	14.2
32735-222	1	9	9	150.4	10.1
32735-223	1	9	1	138.3	16.4
32735-224	1	9	1	159.0	13.6
32735-225	1	9	9	150.8	17.3
32735-226	1	9	1	137.7	13.8

* Feathers are wrapped at each end; the end toward the point is the lower, and that toward the nocked end of the shaft is the upper.

† Point wrapped to stick with #1, and stick to shaft with #3.

‡ Bone barb missing; point consists of pointed stick only.

back to the ground instead of remaining in the animal's body, preventing the shaft from breaking when the animal falls to the ground.

From Table 5, it can be seen that the differences between the two collections, a total of 27 arrows, are not as great in this category. While the juvenile 32735 arrows are shorter, the averages are only 184.64 cm for 32703 to 160.11 cm for 32735. The points show even less of a decrease: 16.46 cm for 32703 versus 15.77 cm for 32735. Of the points, 59% are grooved and 78% are poisoned.

The preferred point wrapping is still cordage type #1, although two points are wrapped with cordage type #3, one with type #4, and another with type #9. Again type #4 is very rare; it utilizes the unusual Z spun *yamaasik* fiber.

Nineteen arrows (70%) use cordage type #9 to wrap the upper end of the feathers. However, 91% of the 32735 collection arrows (10 out of 11) use cordage type #9 while only 56% (nine out of 16) of the 32703 arrows do so. Clearly there is a growing preference for the two ply cotton. Notice, however, that this was not the case on the barbed point arrows; cordage type #9 was less popular on the 32735 feathers than on 32703 feathers.

Table 5.—*Monkey arrows of the Yanomama.*

Accession number	Grooved	Poisoned	Point wrapping	Feather wrapping		Length (cm)	
				Upper	Lower	Arrow	Point
32703-33c	yes	yes	1	9	9	234.5	16.9
32703-88	no	no	1	9	9	158.3	17.7
32730-89	yes	yes	3	1	1	211.3	14.4
32703-90	yes	yes	9	9	9	172.5	11.7
32703-101	no	no	1	1	1	149.0	17.4
32703-102	no	no	1	1	1	164.5	18.2
32703-103	no	?	1	1	1	164.5	18.0
32703-104	no	?	1	1	1	164.5	17.6
32703-105	yes	yes	1	1	1	191.3	15.4
32703-106	yes	yes	1	9	9	183.4	17.7
32703-107	yes	yes	1	1	1	188.3	12.9
32703-108	yes	yes	1	9	9	183.4	17.7
32703-109	yes	yes	1	9	9	196.3	19.0
32703-110	no	yes	1	9	9	161.9	16.1
32703-111	yes	yes	3	9	9	228.4	17.4
32703-112	yes	yes	1	9	9	202.2	15.2
32735-201	yes	yes	1	1	1	158.8	10.6
32735-202	yes	yes	1	9	9	156.8	19.4
32735-204	no	no	1	9	1	161.8	8.9
32735-206	no	yes	1	9	1	159.2	15.4
32735-208	yes	yes	4	9	1	151.3	16.6
32735-212	yes	yes	1	9	9	157.7	17.0
32735-213	yes	yes	1	9	9	177.6	15.8
32735-214	yes	yes	1	9	9	181.0	15.7
32735-215	no	yes	1	9	9	153.9	16.7
32735-216	no	yes	1	9	1	160.3	18.1
32735-218	no	yes	1	9	9	142.8	19.3

The cotton cordage on the lower end is equally popular betwen the two accessions—54% in each.

Lanceolate bamboo points (*xaraka* with *rahoka* point), which are the broadest of the three types, are used on larger game such as tapir, peccary, and deer. Due to the width of the point, the shaft end near the point is unmodified.

Table 6 also indicates that the average arrow length is quite different between the two collections: 200.83 cm for 32703 and 147.92 cm for 32735. This is also reflected in the points, though the difference here is only 1.42 cm (18.86 cm in 32703 and 16.93 cm in 32735).

The preferred *rahoka* point wrapping is still cordage type #1. Cordage type #3 is present on three specimens, and again one arrow utilizes cordage type #9, 2 ply s spin Z twist cotton.

Cordage type #9 is used to wrap the upper ends of the arrow fletching 91.3% of the time; cordage type #1 is used on 8.7% of the upper end feathers.

Table 6.—*Big game arrows of the Yanomama.*

Accession number	Point wrapping	Feather wrapping		Length (cm)	
		Upper	Lower	Arrow	Point
32703-33a	1	9	9	227.5	18.2
32703-84	3	9	1	229.0	21.5
32703-85	1‡	1	1	207.5	24.0
32703-86	1‡	9	9	205.7	14.0
32703-87	1	9	9	184.5	22.6
32703-113	1	9	9	215.5	19.0
32703-114	3	9	9	184.0	18.4
32703-115	1	9	9	198.5	17.6
32703-116	1	9	9	168.5	18.3
32703-117	3	9	9	205.0	21.2*
32703-118	1‡	9	9	225.4	19.8
32703-119	1	9	9	166.7	22.0
32703-120	1	9	9	197.0	20.4
32703-121	1	9	9	217.9	20.5
32703-122	1†	9	9	174.7	9.9
32703-123	1	1	1	196.7	19.4
32703-124	9	9	9	210.0	13.9
32735-200	1	9	9	151.2	11.1
32735-207	1‡	9	1	137.9	14.6
32735-209	1	9	9	150.0	12.1
32735-210	1	9	1	159.2	16.4
32735-211	1	9	9	151.7	11.9
32735-217	1‡	9	1	137.5	16.9

* Shaft broken 73 cm from point end and bound to a new piece of cane with cordage #7.
‡ 32703-118 point decorated on one side with random black paint stripes. 32703-85 and -85 points painted black on one side. 32735-207 and -217 points painted red with *nara.*
† Point end of shaft broken off at one time and re-bound with another point; point itself very small due to re-sharpening.

The lower end feather wrapping again utilizes cordage type #9 on 73.7% of the feathers, while cordage type #1 is present on 26% of the feathers. Due to the imbalance in number of arrows from each collection, comparisons were not made between the 32703 arrows and the 32735 arrows.

From Table 7, it can be seen that the longest class of arrows is the fish and bird arrows. This is unusual; some references (Smole, 1976:

Table 7.—*Mean length of Yanomama arrows.*

	Fish and bird	Monkey	Big game
Accession 32703	207.81 cm	184.64 cm	200.80 cm
Accession 32735	149.61 cm	160.11 cm	147.92 cm
Both accessions	178.71 cm	173.37 cm	174.37 cm

Table 8.—*Mean point length of Yanomama arrows.*

	Fish and bird	Monkey	Big game
Accession 32703	20.14 cm	16.46 cm	18.86 cm
Accession 32735	12.59 cm	15.77 cm	16.93 cm
Both accessions	16.36 cm	16.11 cm	17.89 cm

178) refer to the lanceolate arrows as the longest of the three. However, the big game arrow sample from 32735 (only six arrows) may have had some effect on the class average. The length difference between the collection I and the juvenile collection II arrows is quite large. Fish and bird arrows are 28% shorter, and big game arrows have shortened by 26%. Even the monkey arrows, the least affected by length change, have decreased in size by 13%.

Table 8 depicts the point sizes of each arrow class. As in arrow length, the greatest difference between collections in point length can be seen in the fish and bird arrow class where the points are 37% shorter. The big game points have changed by 10%, and again the least affected are the monkey arrow points, with a size decrease of only 4%. The lanceolate points are the largest of the three by total average. But when

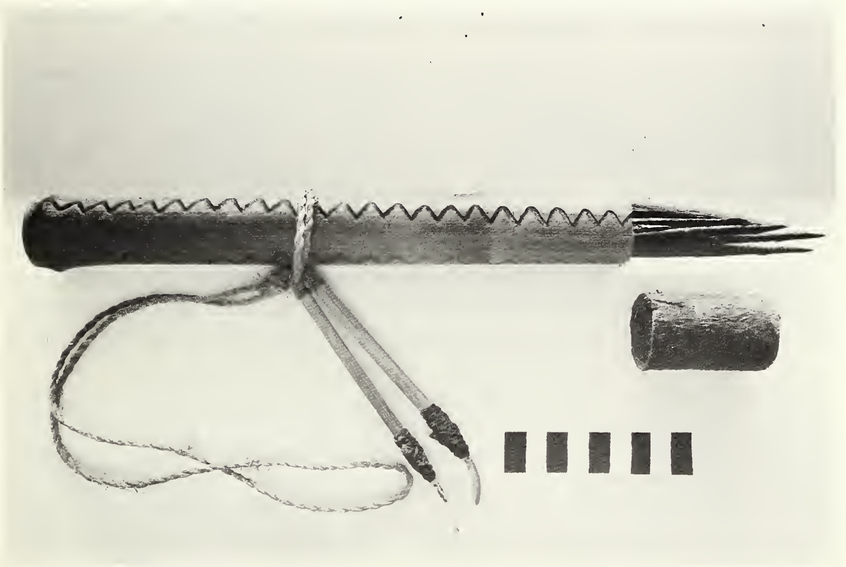

Fig. 10.—A quiver, with the cap off and points protruding.

Table 9.—*Yanomama quivers by neck strap class.**

Class I		Class II	
32703-27a	32703-27b	32703-27e	32703-27g
32703-27c	32703-27i	32703-27h	32703-42a
32703-27j	32703-27k	32703-42b	32703-42d
32703-42c	32703-42f	32703-42e	32703-42k
32703-42g	32703-42h	32703-42l	32703-42n
32735-42i	32735-42j	32703-42o	32703-42r
32703-42m	32703-42p	32735-240	32735-241
32703-42q	32735-321	32735-242	32735-322
32735-323	32735-324		

* Unclassifiable quivers 32703-27d and 32703-27f, discussed earlier, are not included in this table.

calculated by collection, only in 32735 is this the case. In the 32703 collection, the fish and bird points are the longest. The difference between the two types of hunting equipment in collection I and II, juvenile and adult, makes point size calculations between classes difficult.

The following pieces were found when the collection was unwrapped. They may belong together but were not tabulated:

32735-337, lanceolate arrow point, no shaft. Remnants of black paint on one side. L—17.3 cm.

32735-203, arrow shaft, no point. Point fiber wrapping (cordage type #1) still in place. Feathers wrapped with cordage type #9; L—165.3 cm.

*Quivers (*wana*).*—Yanomama quivers are made to carry spare lanceolate big game or palm monkey arrow points, not arrow shafts (Fig. 10). The quiver is made from a single piece of bamboo. A cut is made in the cane just below a joint, which forms a natural closure for the bottom of the quiver. The other end is capped with animal skin from a recently killed peccary, agouti, or monkey. The fresh hide is wrapped around the quiver where it shrinks around the neck for a tight fit. Unmodified agouti teeth (*thom nak*) which dangle from the quiver are used to sharpen the lanceolate bamboo points. The quiver suspends around the neck and down the center of the back, out of the way of the arms when the hunter shoots.

As the analysis of the manufacturing process of the quivers proceeded, it was noticed that quivers can be separated into two classes based on the neck strap attachment; specifically on how the cordage is tied to the quiver after the neck loop is formed. This separation of quivers into classes has no known cultural significance among the Yanomama. The differences are strictly in the manufacturing process.

In Class I, the two ends of the strap are treated individually and each is independently wrapped around the quiver and tied off (32703-27a,

Table 10.—*Yanomama quivers.*

Class	Accession no.	Cordage	Knots	Length (cm)
I	32703-27a	3, 3	A, D, E (3),* C	33.7
	32703-27b	9, 14 (3)	E (2)	31.0
	32703-27c	3	E, Q, F	35.0
	32703-27i	4, 3	D, A (2), L, G, H, C	29.5
	32703-27j	3	I (2), A	36.0
	32703-27k	3	I (2)	33.5
	32703-42c	11 (3), 3	A (5), H, L, J (2), D, ?	33.0
	32703-42f	3	E	32.0
	32703-42g	11 (3), 13 (3)	E (2), A (2)	30.0
	32703-42h	3, 3	E, G, J, H, F, A	28.5
	32703-42i	3, 3	E (2), J, L	31.5
	32703-42j	3, 1	E (2), J, L	31.5
	32703-42m	5, 1	none	31.9
	32703-42p	3, 3	C, E (2), L	33.0
	32703-42q	3, 3	E?, E, L, J, A	33.0
	32735-321	3, 3	E (2), G, ?, J	31.5
	32735-323	3, 9	D, G (2), A, E, C	27.0
	32735-324	?, 3, 3	F, J (3), H (2), C	28.5
II	32703-27e	3	E, A	31.0
	32703-27g	3	J, E	29.5
	32703-27h	3, 3	K, E, G, C	31.0
	32703-42a	5 (3), 3	A (2), C, E (2), G, D	30.1
	32703-42b	16 (4), 3	E (2), A, H, J	30.0
	32703-42d	3, 3	E, D (2), G, A	31.5
	32703-42e	3, 3, 1, 5 (3)	F (2), L (2), A (2)	33.5
	32703-42k	3, 3	A (3), D, E, F	32.9
	32703-42l	3, 2	E, ?, M	27.5
	32703-42n	3, 1	I	35.8
	32703-42o	3, 3	D, F, A (3), E	28.0
	32703-42r	3, 3	E, E?, L, J	28.5
	32735-240	3, 3	E (2), F (2), A (2)	33.7
	32735-241	3, 3	K, A (2), L, J, E	34.6
	32735-242	3	E	27.1
	32735-322	3, 3	G (2), A, E (2), C	27.0
Unclassified	32703-27d	3, 9	F, A (3), H	34.0
	32703-27f	3	F, A	31.0

* The parenthetical number refers to how many of the preceding knot are present on the quiver.

-27b, -27c, -27i, -27j, -27k, -42c, -42f, -42g, -42h, -42i, -42j, -42m, -42p, -42q, 32735-321, -323, and -324). In Class II, the paired ends are treated as a unit; they wrap around the quiver together and are tied off in the same fashion (32703-27e, -27g, -27h, -42a, -42b, -42d, -42e, -42k, -42l, -42n, -42o, -42r, 32735-240, -241, -242, and -322).

The only exceptions to these methods are exhibited by 32703-27d and -27f, which have unique methods of attaching the neck strap. On

Table 11.—*Yanomama quiver knots.*

Knot	Number of quivers with knot	Percent of quivers with knot	Total number of knots	Percent of total knots
A	21	58.3	37	23.6
C*	8	22.2	8	5.1
D	4	22.2	9	5.7
E	26	72.2	38	24.2
F	9	25.0	11	7.0
G	8	22.2	10	6.4
H	6	16.6	7	4.4
I	3	8.3	5	3.2
J	11	30.5	14	8.9
K	2	5.5	2	1.3
L	9	25.0	10	6.4
M	1	2.7	1	0.6

* Knot "B" in this portion of the collection was found only on bows.

32703-27d, one end of the neck strap wraps around the quiver once, loops around both strings in the front of the quiver, and then circles back around in the opposite direction. It then loops around itself in the front again and returns to the back. The two ends are then tied

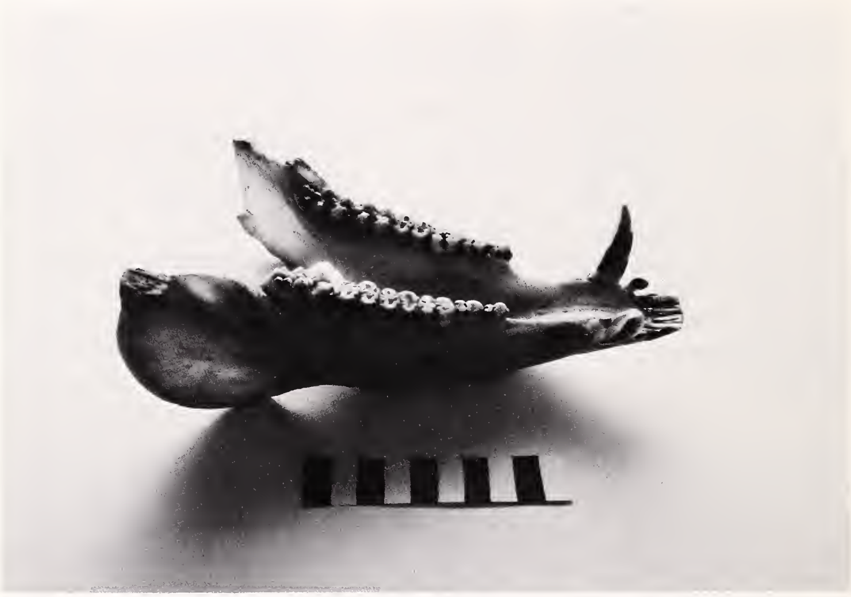

Fig. 11.—A peccary jaw, 32703-17, used like a plane in the final smoothing and shaping of the bow.

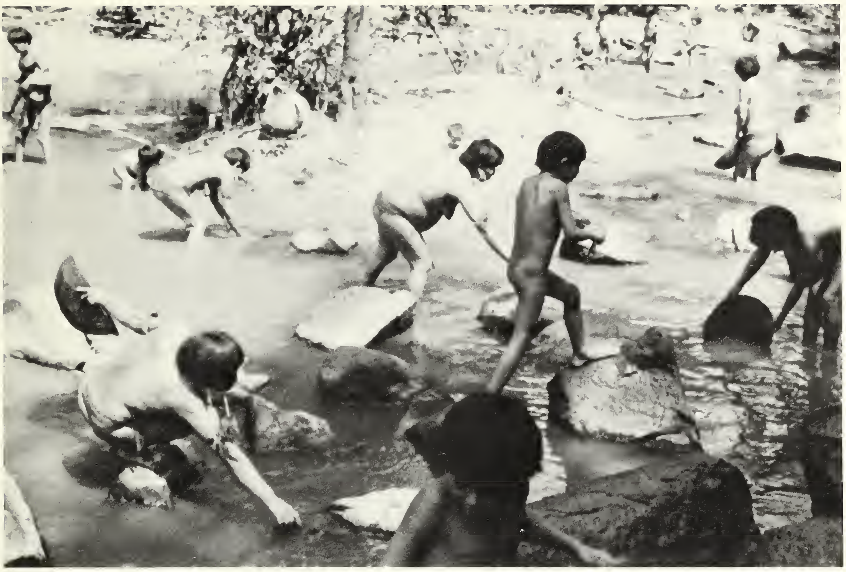

Fig. 12.—Women and children fishing in the river with sieves.

together at the back of the quiver in a square knot and a simple overhand. The neck strap for 32703-27f does not encircle the quiver at all. In this case a band of animal hide cordage, 2 ply final S twist, circles the quiver once and is backwrapped for 1.5 cm. The neck strap passes under this band. It has an unidentifiable knot on one end to keep it from slipping out. The band was fresh rawhide which shrank on the quiver to hold the strap firmly in place.

The agouti teeth are attached to the neck strap in either of two ways. Two teeth are each wrapped onto small sticks or bones (all by cordage type #1), which are then tied onto the neck strap. In one method, one end of a string is tied onto each stick and the bight is then attached to the strap (32703-27b, -27d, -27h, -27i, -42d, -42i, -42j, -42l, -42p, -42q, -42r, 32735-241, -321, -323, and -324). The second method ties one end of the string to one stick, the bight to the next stick, and the other end to the strap. This method can be seen in 32703-42b, -42e, -42g, -42h, -42o, and 32735-322.

From Table 9, it can be seen that the different neck strap attachments are almost evenly divided both in total number of quivers and between collections I and II. Clearly the Yanomama have continued to manufacture both types of neck attachments throughout the 5 year span between accessions 32703 and 32735.

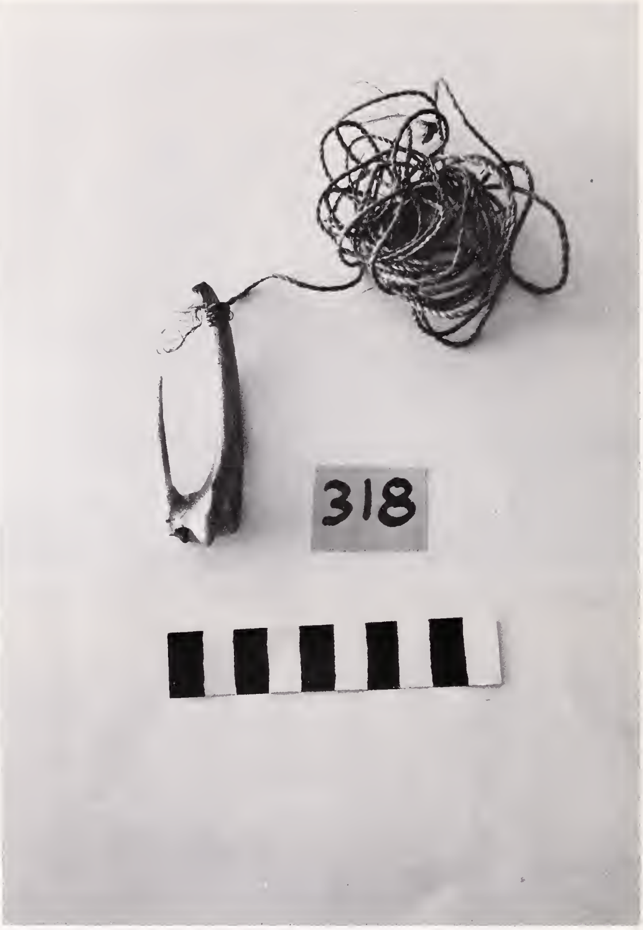

Fig. 13.—Fish hook and line, 32735-318.

Tables 10 and 11 document the cordage and knots used in the manufacture of the quivers. The most popular cordage for the neck strap was type #3—the two ply s spin Z twist *yamaasik* fiber. This was used on 33 of the 36 quivers (92%). Of the 67 different pieces of cordage present on the quivers, 49 pieces, 73%, were cordage type #3. Four pieces (6%) were type #1, and three pieces (4%) were each types #5(3) and #9. Type #13 was present in two pieces, and types #2, 4, 13(3), 14(3), and 16 were present as one piece each. Eight pieces of cordage (12.1%) were cotton, while the other 59 (88%) were *yamaasik* fiber.

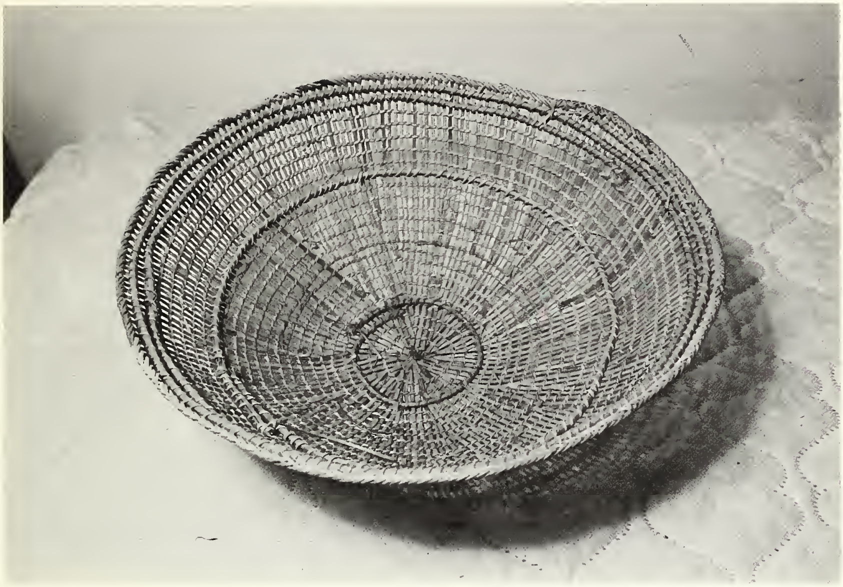

Fig. 14.—A sieve basket used in fishing.

The most complex cordage found on a quiver was the three ply S spin Z plied cotton with a final S twist, type #14(3), on 32703-27b.

Knot "E" was used on the greatest number of quivers, present on 72.2% of the specimens. The second most utilized knot was "A"; 58.3% of the quivers in the collection featured at least one. Third was the half hitch, knot "J," on 30.5% of the quivers. Tied for fourth place are knots "F" and "L," the square knot and the wrap, both of which occur on 25% of the quivers.

Of the total number of knots tied, "E" is still the most popular with 24.2% of the total. The knot with the second highest rate of usage, "A," accounted for 23.6% of the total. Although these percentages are so close as to make the difference unremarkable, a second examination of the percentage of quivers using the two is telling. Only 58.3% of the quivers used knot "A," while 72.2% used knot "E." Thus, nearly all of the men make quivers with at least one knot "E," while slightly more than half make quivers with knot "A." The third and fourth highest percentages, knots "J" and "F," were 8.9% and 7% respectively. Thus, two knot ("E" and "A") account for almost half (74 out of 157, 47.7%) of the total knots used on the quivers while a host of other ties compose the other half.

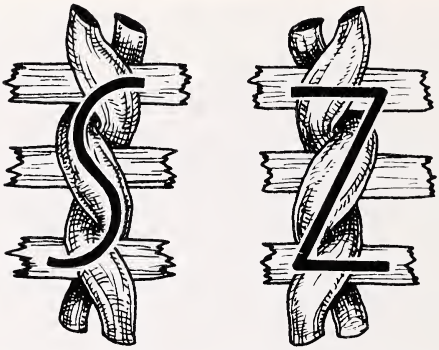

Fig. 15.—S and Z twist stitch slant in basketry. Note that this illustration is drawn at a 90° rotation from the normal; the warps here are horizontal rather than vertical as they would be in a properly oriented specimen (see Fig. 20).

There seem to be no differences in quiver construction between the two accessions. The cordage stays the same, the knots undergo no changes, the sizes remain standard, and the classes based on neck strap attachment are evenly divided.

*Peccary jaws (*warenak*).*—These unmodified lower jaws with the teeth still intact (Fig. 11) are used like a plane for the final smoothing and shaping of the bow.

32703-17, collected in 1979 from Iropitheri village. L—21.0 cm W—11.0 cm.
32703-48, collected 1979–1980. L—21.5 cm W—9.5 cm.

*Beeswax cakes (*puunaxi*).*—These lumps of beeswax are used to coat *yamaasik* fibers, and sometimes cotton yarns. The beeswax acts as a preservative, preventing the strands from splitting and rotting.

32703-30A, collected in Hewenahipiutheri village, 12/1979; L—15.5 cm.
32703-30B, same as 32703-30A; L—15.0 cm.

Fishing Implements

The Yanomama make less use of riverine resources than do other Amazonian Indians. Fiber line fishing is rarely successful; native fishing lines are made of twisted fibers, highly visible to the fish. Piranhas in the river see the line and bite it off. However, fish are a popular food. Shallow streams are dammed and narcotic lianas are put into the water (Chagnon et al., 1971:72–74). The small stunned fish are scooped out by the women and young girls with baskets (Fig. 12), while the boys shoot the larger ones with a bow and fish and bird arrow.

*Fish hooks (*opo maro*) and lines (*yamaasik*).*—As stated previously, these are impractical due to their high visibility. Their only use is in

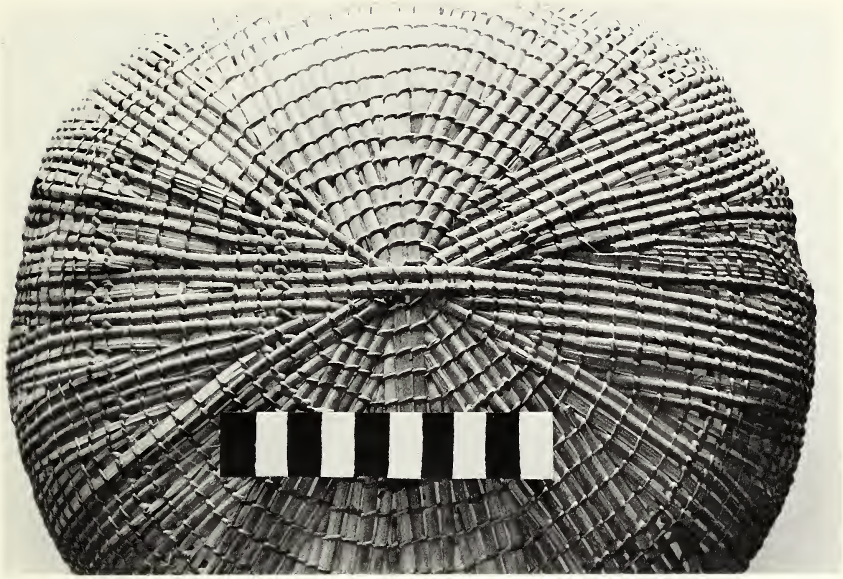

Fig. 16.—Detail of a sieve center, showing the 2 over 2 warp arrangement and the initiation of twining.

ponds or lakes with no piranhas. These specimens (Fig. 13) were made for Carnegie Musuem of Natural History at the request of the collector in 1984.

32735-318, cordage type #3 attached to an armadillo bone by knots "J" and "M"; L (line)—330.0 cm L (hook)—8.3 cm W (hook)—2.7 cm.
32375-319, two armadillo bone fish hooks tied together via a hole drilled though the bone. The line is composed of cordage type #3; a large knot ("A") keeps the line from slipping through the hole. L (line)—290.0 cm; (hooks)—6.0 cm & 5.5 cm. W (hooks)—2.3 cm & 2.6 cm.
32735-320, armadillo bone fish hook without line; L—8.4 cm W—2.5 cm.

*Sieve baskets (*ikatom*).*—These baskets (Fig. 14), made by women of *masik* vine, are an example of the dual use category. Their main use is in fishing; women and children use sieves to scoop small stunned fish out of the river after it has been poisoned by the addition of narcotic vines. Sieves can also be used to squeeze prussic acid from manioc pulp or to sieve manioc flour in preparation for cassava bread.

The baskets are remarkably standardized in construction. Not only are the wall and rim types the same, but normally individualistic attributes such as splices are also very similar. All baskets are simple open twining with an S twist stitch slant (Fig. 15). Center warps are

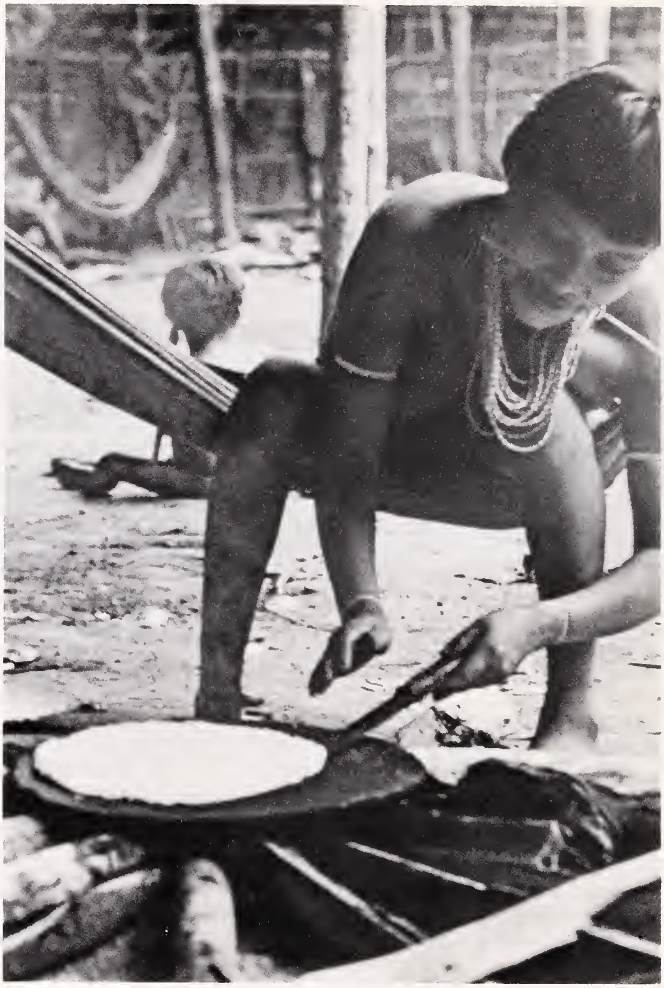

Fig. 17.—Yanomama woman baking cassava bread on a clay dish over the fire.

either two over two in a "+" or one over one in an "X" (Fig. 16). Twining is always initiated by folding the weft in half over one of the center warps and proceeding in a circular (clockwise) fashion from this point. In two places (five to seven courses from the center and 10 to 19 courses from the center) an extra rigid weft is added to the inside, wrapped to either another course of twining or a semi-rigid weft on the outside, to reinforce the wall. This is the case for every sieve except 32703-39, which has no wall reinforcements. In the analysis this paired

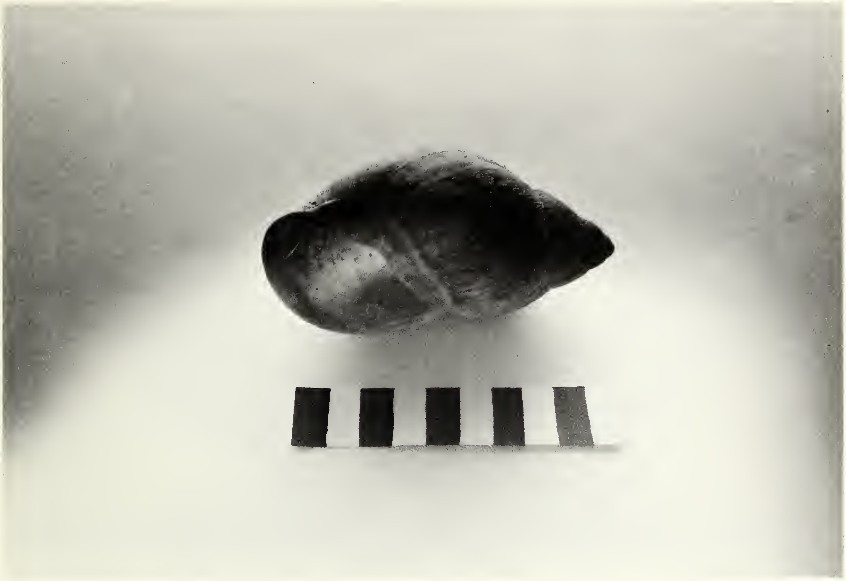

Fig. 18.—A snail shell (*Melagalobulimus oblongus*), 32703-19, used to smooth clay dishes prior to firing.

element is referred to as the "paired outer element." Rims are always finished with two courses of wrapped twining around an extra (rigid) weft (wrapped on as previously discussed) and a false braid (over the last row of twining on the cut warp ends) in which a stitch is occasionally wrapped down onto the last rigid weft to secure the rim onto the basket. New warps are added by inserting a new stitch on all sieves except 32703-2C. This basket adds new warps by inserting them into previously existing weft crossings. Splices have the ends of both the new and exhausted wefts bound under the previous or next stitch respectively on the inside of the basket on every sieve except 32703-39. Four different types of splices are present on this basket. While 30% of the splices follow the standard established on the other baskets, the other 60% are divided between three other splices. One splice starts both the new and exhausted wefts at the same point on the inside of the basket, another starts the new splice on the outside of the basket, and the third leaves the exhausted weft on the outside of the basket.

32703-1, bought from a Maxikopiutheri village woman in November 1979. Center: two over two Wrapped twining: 5 and 17 courses from the center. Paired outer element is twining. Flexible wrapping weft terminated by knot "A" around rigid weft. Measurements: D—36.0 cm H—13.0 cm.

32703-2A through C were bought from Maxikipiutheri and Hewenahipiutheri village women in December 1979.

32703-2A Center: one over one Wrapped twining: 5 and 12 courses from the center. Paired outer element is twining. Flexible wrapping weft terminated by knot "A" around the rigid weft. Measurements: D—37.5 cm H—16.5 cm.

32703-2B Center: two over two Wrapped twining: 5 and 12 courses from the center. Paired outer element is both twining and a semi-rigid weft. Flexible wrapping weft terminated by knot "A" around the rigid weft. Measurements: D—43.0 cm H—17.5 cm.

32703-2C Center: 2 over 2 Wrapped twining: 6, 16, and 38 courses from the center. Paired outer element is twining. Measurements: D—45.0 cm H—18.5 cm.

32703-39 Center: 2 over 2 Wrapped twining:none. Paired outer element (on rim wrapped twining) is a semi-rigid weft. Measurements: D—25.0 cm H—13.0 cm.

32735-180 Center: two over two Wrapped twining: 6 and 13 courses from the center. Paired outer element is twining; flexible wrapping weft terminated by knot "A" around the rigid weft. Measurements: D—36.0 cm H—13.8 cm.

32735-243 Center: two over two Wrapped twining: 7 and 19 courses from the center. Paired outer element is twining; flexible wrapping weft terminated by knot "A" around the rigid weft. Measurements: D—42.0 cm H—18.5 cm.

HOUSEHOLD ARTICLES

Household articles are those items that are intended for use in the home. This is a loosely defined category, but generally includes all artifacts used in food preparation, eating, sleeping, or house maintenance activities. Again distinctions are, in some cases, arbitrary. Multiple use items are placed in the category of their primary function.

Food Storage, Preparation, and Serving

Traditional methods of food preparation relied heavily on clay pots and dishes. These clay items are being replaced by aluminum utensils acquired through trade with Westerners. But food is still stored in woven bowl baskets, and gourd serving implements and fingers have not been replaced by silverware.

*Clay pots (*hapoka*).*—Pots are used to stew meat and other foods over the fire. They are made by coiling the clay upward, and smoothing it inside and out with a snail shell. They are heavy—1 cm thick at the sides—and taper off to .25 cm at the out-turned rim. Dried inside the house, and fired by piling brush around them (Chagnon, 1977:20), they are fragile and cumbersome to use and carry. Temper can be, and usually is, a variety of substances (shell, different types of grit), all in the same pot.

32703-53, collected 1979–80. Broken in 13 pieces. D—26.55 cm H—22.0 cm.

32735-88, rounded bottom with many scratches, leans to one side when standing. D—17.5 cm H—19.0 cm.

32735-89, fire blackened, rounded bottom, leans to one side when standing. D—17.5 cm H—18.9 cm.

32735-90, fire-blackened, rounded bottom, leans to one side when standing. Food residue inside, one small crack near base. D—26.6 cm H—24.8 cm.

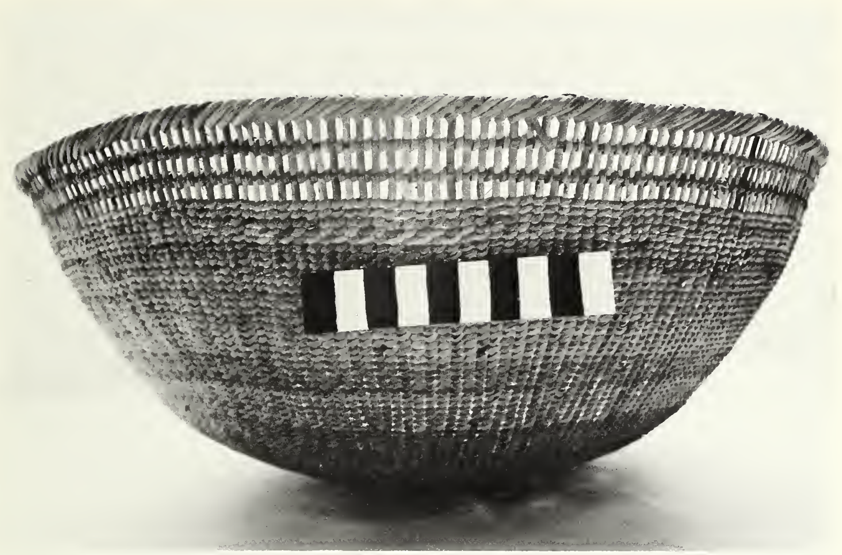

Fig. 19.—A bowl basket used to collect, store, and serve food.

*Cassava griddles (*mahe*).*—These are also made of clay which is coiled and smoothed with a shell. The particular example in the Carnegie Museum of Natural History collection is a girl's toy griddle. The actual woman's griddle, used for baking cassava bread (Fig. 17), is many times larger.

32735-87, round dish, fire blackened. D—16.4 cm H—0.7 cm.

Snail shell.—This shell (Fig. 18) is that of the largest land snail in South America, *Melagalobulimus oblongus.* It is used to smooth the clay prior to firing.

32703-19, from Wakathautheri village, collected March 1980. L—11.0 cm W—5.5 cm.

*Bowl Baskets (*xotehe*).*—These are all purpose baskets among the Yanomama (Fig. 19). They are twined by women from *masik* vines in a variety of sizes, and are used mainly to store and collect foods in the home. Often decorated, the paints are manufactured from leaves and seeds from cultivated bush trees. Painted designs are usually shades of red, orange, or black in patterns of circles, dots, or serpentine lines.

The baskets are close simple twining with an S twist stitch slant (Figs. 15 and 20). Centers are either 2 over 2 in a "+" or 1 over 1 in an "X." In all but two cases, the direction of twining is clockwise. Dec-

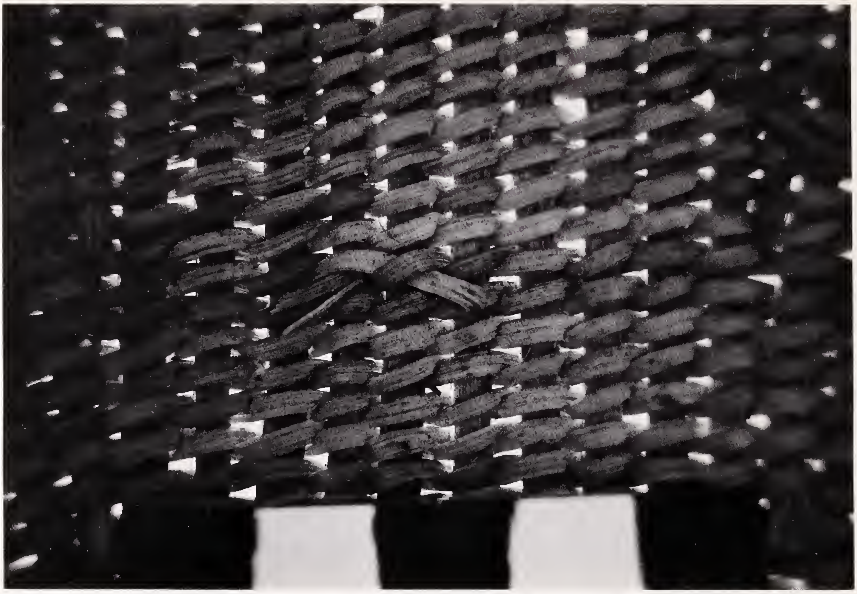

Fig. 20.—Detail of twining on a bowl basket, with the warps in their proper vertical alignment. This photograph also shows the standard weft splice, with the new and exhausted wefts bound under the preceding and next stitches respectively on the inside of the basket.

orations are added by twining with differentially dyed wefts or painting directly on the basket wall.

The standard method of new warp insertion is via addition of a new weft crossing. The alternative is to insert the new warp end in one or more pre-existing weft crossings. Standard weft stitch splices (Fig. 20) bind the new weft under the previous stitch crossing on the inside of the basket while the exhausted weft is bound under the next stitch crossing on the inside. There are two variations to this standard method; variation #1 has the new stitch stub protruding on the outside of the basket, occasionally bound under a bulging stitch, while the exhausted weft protrudes on the inside. In variation #2, the new and exhausted wefts begin and end in the same place on the inside without binding under any stitches.

All of the baskets have one or two courses of wrapped twining at the rim (Figs. 21, 22, 23, and 24). This wrapped twining is an unusual variation of the standard form (see Adovasio, 1977:18). Rather than wrapping the rigid weft directly to the warps with the flexible weft stitch, either an extra semi-rigid weft (Fig. 24) or a row of twining (Fig. 22) is applied to the outside of the basket. The rigid weft parallels this

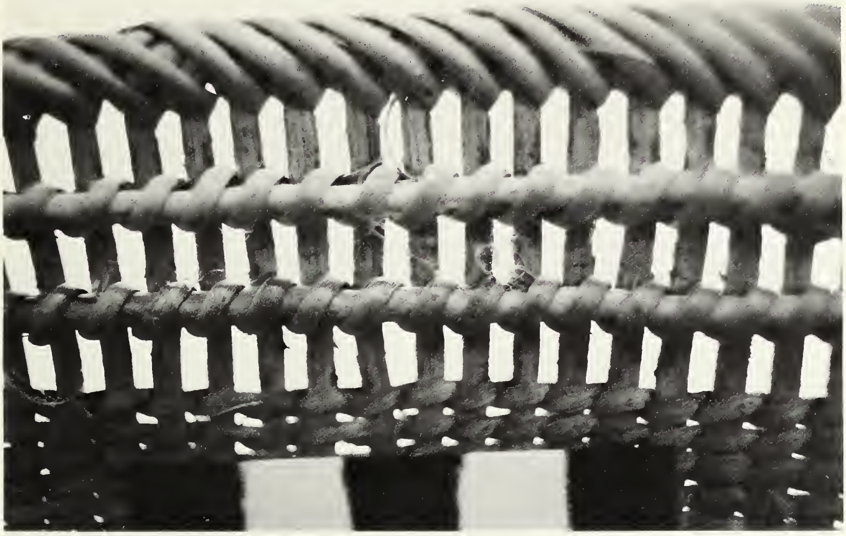

Fig. 21.—Detail of wrapped twining from the inside of the basket. Rim finish is the standard false braid.

row on the inside. The flexible weft stitch then wraps the rigid weft to its partner on the outside, and this partner to the warps. The rim is finished off with a course of twining on the cut warp ends. In all but three cases a false braid is then applied (Figs. 21 and 24), from which an occasional stitch drops down to the last rigid weft to secure the braid onto the basket.

In two of the three exceptions to the false braid (32703-4a and -4e), the top row of twining on the cut warp ends and the next row of wrapped twining around the rigid weft is wrapped in a parody of coiling (Fig. 23). This loose coil occasionally drops down to include the first row of wrapped twining. 32703-3a exhibits another form of rim. It has the normal two courses of wrapped twining around a rigid weft and the last row of twining on the cut warp ends, but no false braid. The rim finish consists of an extremely tight figure-of-eight wrap around every two to three warps, with an occasional wrap to the last rigid weft (Fig. 22).

Table 12 depicts manufacturing data of the bowl baskets. All of the baskets from accession 32703 begin clockwise, while two from accession 32735 begin counterclockwise. Three of the 32703 baskets (14.3%) have a 1 over 1 center, while the rest (85.7%) have the standard 2 over

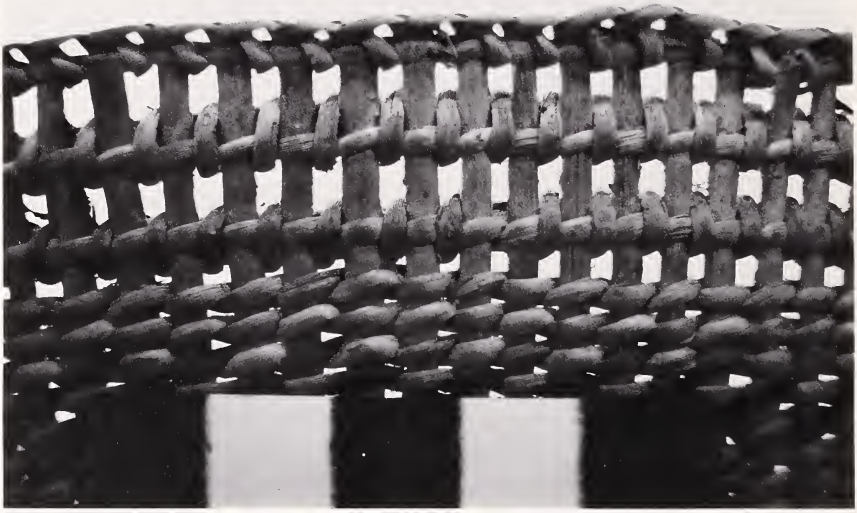

Fig. 22.—Detail of wraped twining from the outside of the basket. The paired outer element is twining. The basket features the figure-of-eight rim finish.

2 center. Three of the 32735 collection centers (12.5%) were 1 over 1, one was 1 over 2 over 1, and one had 4 warps in a random arrangement. The remainder of the centers (87.5%) were standard 2 over 2.

The standard warp insertion (new warps in new weft crossings) was utilized by 57% of the 32703 baskets, while 19% used the alternate method (new warps in pre-existing weft crossings), and 23.8% exhibited a combination of both methods. In the later 32735 accession, 58% of the baskets had standard warp insertions, 20.8% used the alternate method, and 16.6% exhibited a combination of both.

The greatest differences between collection I and II baskets are seen in the weft splices. While only one 32703 basket had a splice other than standard (5% variation #2), 45.8% of the 32735 baskets utilized non-standard splices. In this collection, 20.8% of the baskets were a combination of the standard splice and variation #1, variation #1 alone was also seen in 20.8% of the baskets, and one basket was a combination of variations #1 and #2.

Three of the baskets from collection I used one instead of two courses of wrapped twining at the rim, while all of the collection II baskets had two courses. All of the 32703 baskets paired the rigid weft with twining, but 33% of the 32735 baskets paired a semi-rigid weft on the outside

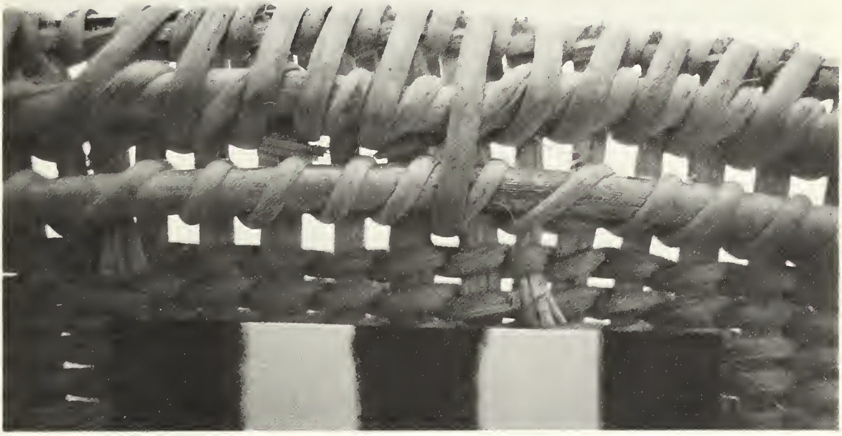

Fig. 23.—Detail of a coiled rim finish from the inside of the basket.

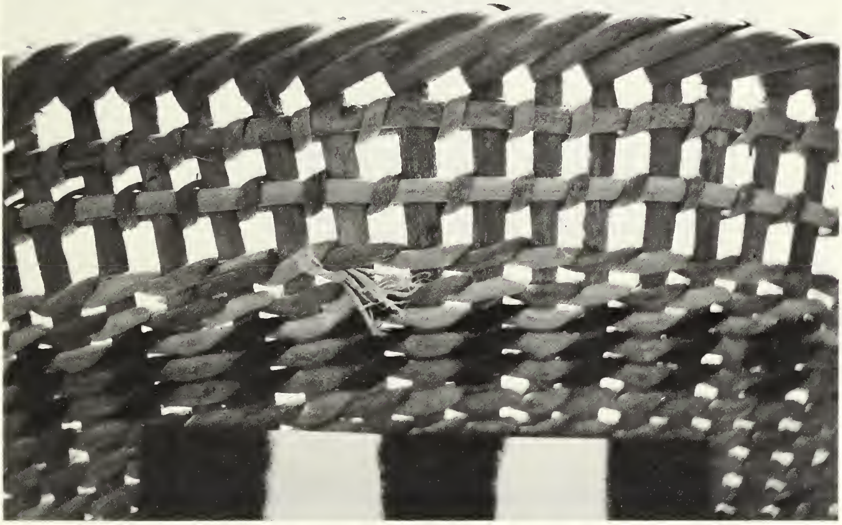

Fig. 24.—Detail of wrapped twining from the outside of the basket. The paired outer element is a semi-rigid weft. The basket features the standard false braid rim finish.

Table 12.—*Bowl baskets of the Yanomana.*

Accession number	Center	Warp insertions	Weft splices	Wrapped twining			Measure (cm)	
				No. of courses	With twining?	With semi-rigid weft?	Diameter	Height
31996-1	2 over 2	standard	standard	2	no	yes	43.0	15.6
32703-3A	2 over 2	30% standard	standard	2	yes	no	36.0	15.4
-3B	2 over 2	standard	standard	2	yes	no	37.1	12.4
-4A	2 over 2	standard	standard	2	yes	no	30.9	12.5
-4B	1 over 1	standard	standard	2	yes	no	23.9	9.6
-4C	2 over 2	standard	standard	2	yes	no	24.0	12.1
-4D	2 over 2	alternate	standard	2	yes	no	29.0	10.6
-4E	2 over 2	standard	standard	2	yes	no	32.3	11.5
-4F	2 over 2	40% standard	standard	2	yes	no	35.4	16.5
-37A	2 over 2	alternate	95% standard 5% var. #2	2	yes	no	16.1	7.4
-37B	2 over 2	standard	standard	2	yes	no	20.4	10.8
-37C	2 over 2	50% standard	standard	2	yes	no	25.5	7.4
-37D	2 over 2	alternate	standard	1	yes	no	23.4	9.3
-37E	2 over 2	10% standard	standard	2	yes	no	23.1	8.9
-37F*	1 over 1	30% standard	standard	2	yes	no	30.2	12.4
-37G	2 over 2	standard	standard	2	yes	no	31.4	13.6
-38A	2 over 2	standard	standard	1	yes	no	17.1	5.9
-38B	2 over 2	standard	standard	1	yes	no	19.2	7.8
-38C*	2 over 2	standard	standard	2	yes	no	24.0	8.9
-38D	1 over 1	standard	standard	2	yes	no	23.9	9.8
-38E	2 over 2	standard	standard	2	yes	no	31.0	13.5
-38F	2 over 2	alternate	standard	2	yes	no	41.6	16.4
32735-169	1 over 1	standard	50% var. #1 50% var. #2	2	no	yes	15.0	6.2
-170	2 over 2	alternate	97% standard 3% var. #1	2	yes	no	15.1	5.8
-171	2 over 2	standard	variation #1	2	no	yes	16.7	8.9
-172‡	1 over 1	standard	variation #1	2	no	yes	17.2	6.4

Table 12.—*Continued.*

Accession number	Center	Warp insertions	Weft splices	Wrapped twining			Measure (cm)	
				No. of courses	With twining?	With semi-rigid weft?	Diameter	Height
-173	2 over 2	standard	25% standard 75% var. #1	2	no	yes	19.2	7.7
-174‡	1 over 2 over 1	90% standard	standard	2	yes	no	19.5	9.5
-175								
-176	2 over 2	standard	standard	2	yes	no	30.7	11.8
-177	2 over 2	alternate	variation #1	2	no	yes	33.0	12.4
-178	1 over 1	standard	60% standard 40% var. #1	2	no	yes	30.0	11.3
-179	2 over 2	standard	75% standard 25% var. #1	2	yes	no	43.0	15.6
-181	2 over 2	50% standard	standard	2	yes	no	19.1	12.1
-182	2 over 2	standard	standard	2	yes	no	21.9	9.1
-183	2 over 2	standard	40% standard 60% var. #1	2	no	yes	24.5	9.5
-184	4 warps, random	standard	standard	2	yes	no	25.7	12.4
-185	2 over 2	50% standard	standard	2	yes	no	23.9	12.3
-186†	2 over 2	standard	variation #1	2	no	yes	28.4	12.7
-187	2 over 2	alternate	standard	2	yes	no	42.5	14.9
-188	2 over 2	50% standard	standard	2	yes	no	52.4	19.3
-239	2 over 2	standard	variation #1	2	yes	no	18.5	7.5
-244	2 over 2	alternate	standard	2	yes	no	43.8	18.0
-245	2 over 2	standard	standard	2	yes	no	47.0	17.5
-302	2 over 2	standard	standard	2	yes	no	28.5	14.0
-333	2 over 2	alternate	standard	2	yes	no	20.1	12.3

* Food residue inside basket.

‡ Twining begins counterclockwise.

† 2 ply bark fiber tied through rim with knot "H."

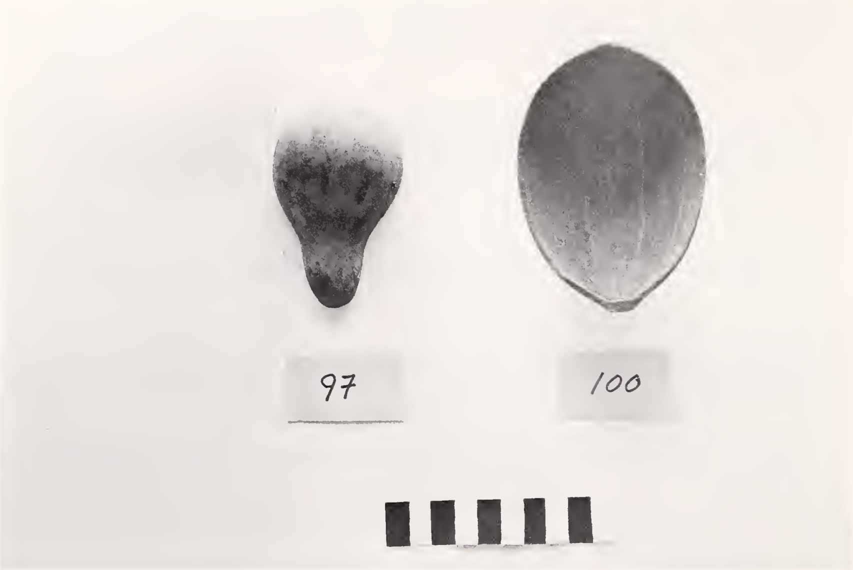

Fig. 25.—Cup (left) and spoon (right), accession #32735.

with the rigid weft on the inside. All of the 32735 baskets had a false braid on the rim, though three of the 32703 baskets did not.

One basket in this category comes from neither collection I or II. This was a purchase by the Section of Anthropology from the Carnegie Museum of Natural History Gift Shop in 1982. This Yanomama basket thus probably dates from the same time period of both collections, though there is no way of knowing if the basket was manufactured by the Yanomama at that same time. With the exception of the semi-rigid weft instead of twining paired with the rigid weft, it is standard "across the board" (standard warp insertions and weft splices, 2 over 2 center, and 2 courses of wrapped twining).

Overall, the collection I baskets show much less variation than the collection II. Eight of the 32703 baskets (38.1%) are standard "across the board" (2 over 2 center, standard warps and wefts, and 2 courses of wrapped twining paired with twining). This is particularly true of the weft splices, where only 1 basket exhibits a non-standard splice. By contrast, only 16.6% of the 32735 baskets are standard "across the board," with fully 45.8% of the baskets utilizing non-standard splices. Variation #1, never seen in the earlier baskets, is present on all of the non-standard 32735 baskets. However, all of the collection II baskets had the false braid rim while three of the 32703 had unusual variations.

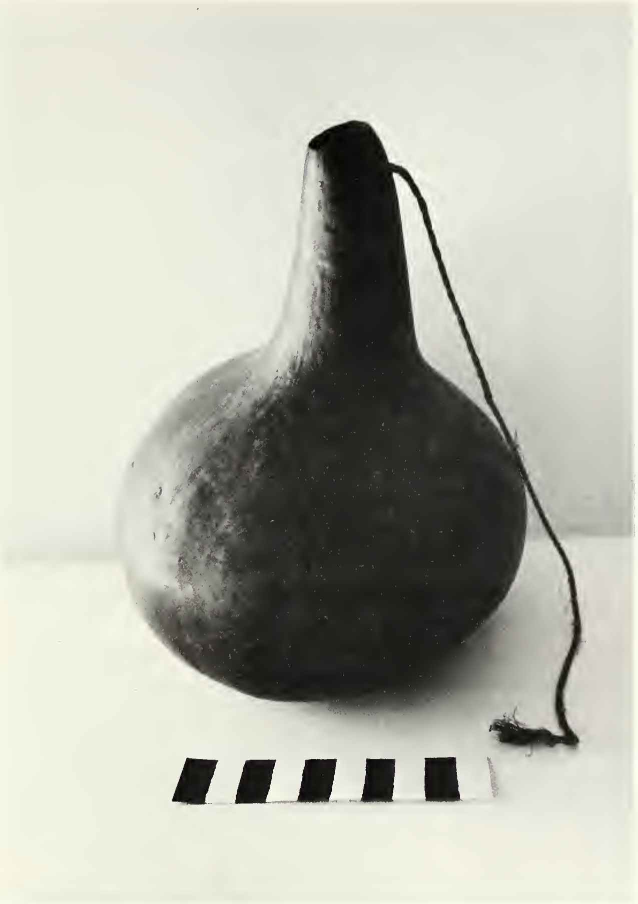

Fig. 26.—Gourd (32703-21B) used for water storage in the home.

The bowl baskets of accession 32735, notwithstanding the rims, are much less rigid in manufacture than the previous accession. Warp and weft splices show much more variation and the wrapped twining is often paired with a semi-rigid weft, another innovation. The 2 over 2 center is less common, and random centers make an appearance for the first time in accession 32735.

Cups, spoons, and gourds.—Cups and spoons (Fig. 25) are both made from halved gourds (possibly *Lagenaria siceraria*; J. Freccione, personal communication). Cups are made from gourds with a pinched neck, while spoons are entirely oval. Both are used for the same purpose:

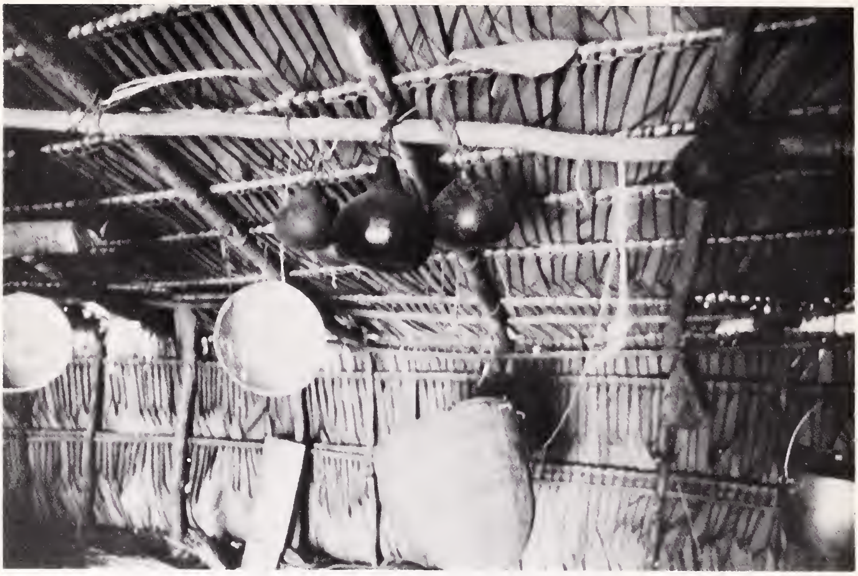

Fig. 27.—Hanging storage of gourds and baskets in a Yanomama house.

to scoop out water or food from another dish. Whole gourds in this category are used to store water.

32735-9, cup (*mau hesi ihiru*), hollowed and burned out. L—11.7 cm W—9.0 cm.
32735-45, same as 32735-9. L—13.4 cm W—8.7 cm.
32735-95, same as 32735-9. owned by Pinicius. L—8.3 cm W—4.9 cm.
32735-96, same as 32735-9. L—9.2 cm W—5.8 cm.
32735-97, same as 32735-9. L—9.3 cm W—5.6 cm.
32735-98, same as 32735-9. L—8.4 cm W—5.1 cm.
32735-101, same as 32735-9. L—14.4 cm W—11.4 cm.
32735-99, spoon (*yarimariaxi*), oval, yellowish brown in color. Hollowed and burned out. L—11.4 cm W—7.7 cm.
32735-100, same as 32735-99. L—11.3 cm.

Whole gourds (*horokoto*) are used for water storage inside the home. The top of the gourd is cut off, and a small hole is drilled near the cut. A string is threaded through the gourd and knotted on the end to hold it inside (Fig. 26). The gourd is then hung inside the house for use when needed (Fig. 27).

32703-21A, string: cordage type #3 with tight knot "A" and loose knot "J" on end; held inside gourd with same on other end. Gourd length—15.0 cm.
32703-21B, same as 32703-21A but one string end only knot "A." Held inside gourd with knots "G" and "A." Gourd length—19.5 cm.
32703-21D, string: cordage type #12(5) tied at each string end with knot "A." Gourd length—22.3 cm.

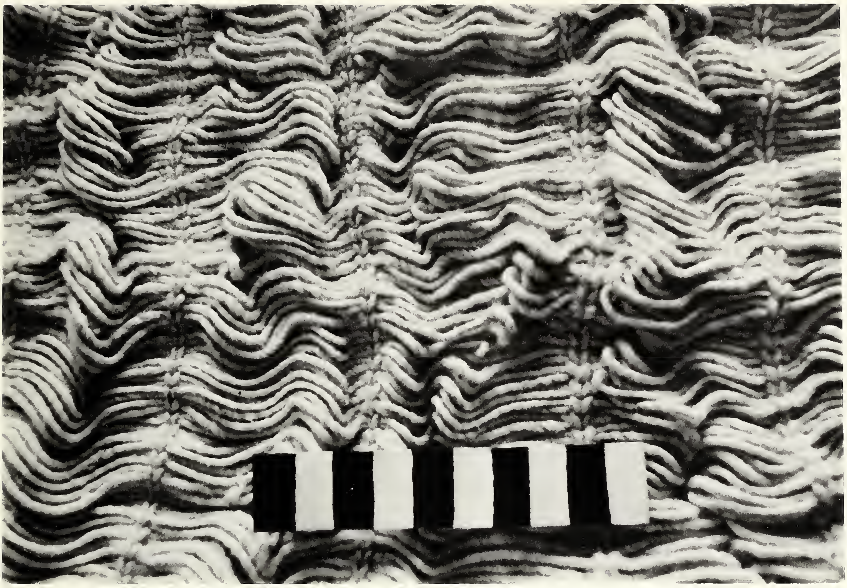

Fig. 28.—Detail of the twined wefts on a cotton hammock, 32735-1.

32703-51, six gourds threaded on cordage type #10; knot "A" on one end. L (of longest gourd)—19.0 cm L (of shortest gourd)–14.0 cm.

32735-94, string: cordage type #1 folded in half and twisted into cordage type #3. Knot "A" holds string inside gourd. Gourd length—18.4 cm; string length—40.7 cm.

32735-325, two gourds tied together with cordage type #3 in a bow. Knot "A" on one gourd inside, knot "E" on the other. Both string ends finished off in knot "A." L (longer gourd)—18.1 cm L (shorter gourd)—16.8 cm.

Hammocks

All Yanomama sleep in hammocks strung as close to the fire as possible, frequently in stacked rows. Children often sleep with their mothers until three years of age.

Three types of hammocks are made, of which the cotton is strictly for household use. The other two, of vine and bark, are used likewise but the bark hammocks are also made by men on the spot during overnight camping trips.

*Cotton hammocks (*rakamothok*).*—These are usually made by women, though occasionally a man will assist during the final stages of manufacture if the hammock is for him. They are made of cultivated cotton; the yarns are spun by Yanomama women. The horizontal warps consist of one strand of cotton yarn, wrapped repeatedly around two poles set in the ground a convenient distance apart. Paired courses of

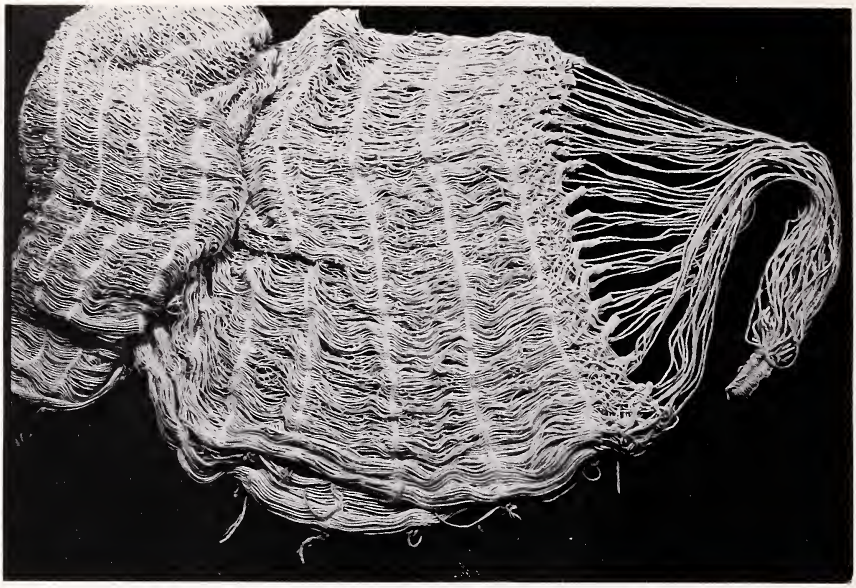

Fig. 29.—Cotton hammock, 32703-24A. Note the plaited border.

vertical wefts are then twined, one in a Z slant and the other in an S slant (Fig. 28), at 3 to 9 cm intervals. The warp ends are tied together with a length of cordage, the poles are removed, and a longer string of fiber or cotton is added at each end to tie the hammock to a pole or tree.

32703-24A, collected from FUNAI post at KM 49.50 of Brazilian Highway BR 210 18 March, 1979. Approximately 840 warps, cordage type #2, held together with paired S and Z slant twining rows every 3 to 7 cm. Hammock body approximately 89 cm long, with a plaited (2:2) border 6 cm wide each end (Fig. 29). Warp strands then folded over into loops; type #13(3) cordage threaded through all loops and used as a suspension rope. Tied end of suspension rope wrapped tightly with Z twist cotton and stitched into small loop to be slipped over hanging peg or pole. L—177.8 cm.

32735-1, approximately 550 cordage type #11(3) warps held together with 2 courses of twining (one S slant and one Z slant) every 7–9 cm. Wefts are initiated on one side of the hammock with all four plies tied as a unit in a simple overhand; each weft course tied off on other side using one knot "A" or one knot "G" with one knot "A." Suspension string is cordage type #6(4); ends tied together at each hammock end with knot "F." Three of the four string ends finished off in knot "A" (one ply around other three). L (hammock only)—122.0 cm.

*Vine hammocks (*toothothok*).*—These are made by men of the same *masik* vine as the baskets. Notice that there are no weft courses in the body of the hammock to hold the vines together.

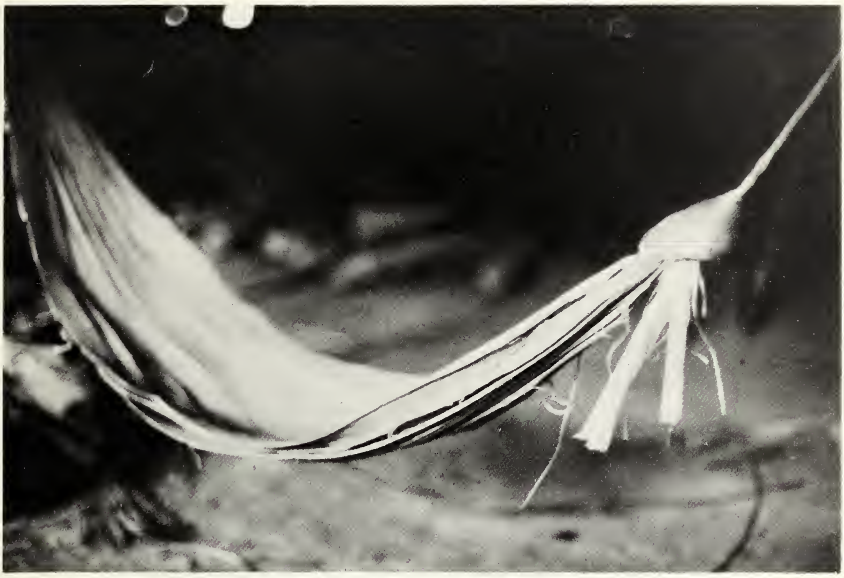

Fig. 30.—A bark hammock hanging inside a Yanomama house.

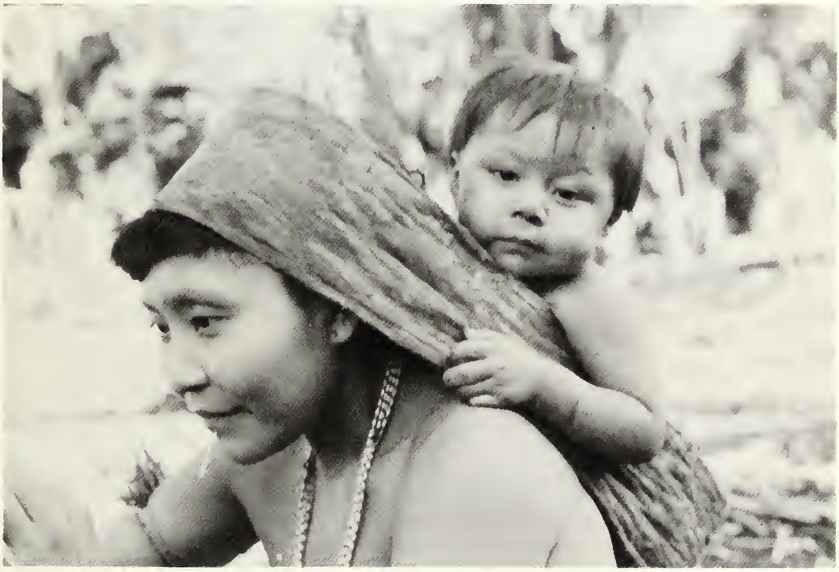

Fig. 31.—Yanomama woman holding a baby on her back with a bark baby carrier.

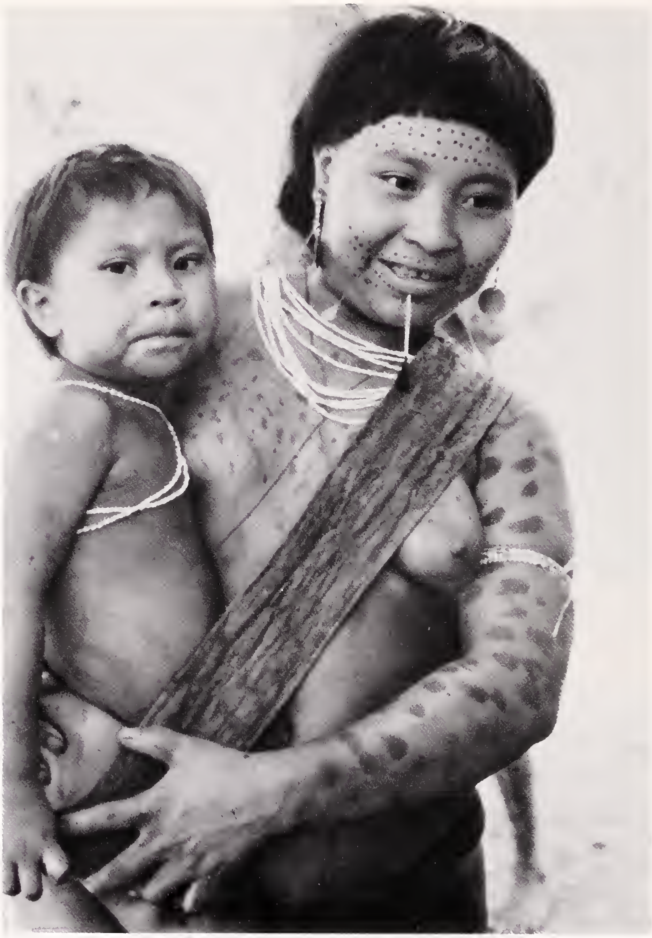

Fig. 32.—Yanomama woman holding a baby on her hip with a bark baby carrier.

32703-24B, collected from Mahuku-nanesim of Hewenahipiutheri village in December 1979. Approximately 200 warps held together 11–12 cm from each end with cordage type #12(5). Tied on one end in knot "G," three knots "A"s, and knot "F." The other end has type #3 cordage tied in two knot "A"s. The warp ends are bundled together, tightly wrapped with type #3 cordage, and clipped 4 cm after the wrap. On one end a suspension rope is formed from seven strands of type #3 cordage, with two of the strands finished off with knot "A." The other suspension rope is composed of four strands of type #3 cordage and one strand of type #6(4) cordage, with all ends finished off in knot "A."

*Bark hammocks (*rainathethok*).*—Bark strips averaging 7 cm in width are cut, folded over, and tied at the ends with a length of cordage (Fig. 30). Like the vine hammocks, no weft crossings hold the strips together. These hammocks are also made by men, most commonly on the spot during overnight hunting trips.

32703-47, made for collector in December 1979. 8–10 bark strips folded over on ends, wrapped, and secured with 2 ply z spin S twist bark cordage tied in knot "A" around the strips. Cordage ends finished off with knot "A" (one ply around the other). L—43.4 cm.

*Baby Carriers (*rainathe*)*

The straps, composed of the same tree bark as the third type of hammock, are made and used by women to carry babies in one of two fashions. The bark strap can pass across the forehead like a tump line with the baby on the back (Fig. 31), or it can pass over one shoulder and suspend the baby on the opposite hip (Fig. 32).

32703-26A, from Ixinapirim of Wakathautheri village March 1980. One continuous band of bark stitched twice across the ends with cordage type #3 tied off in knot "G." D—54.5 cm W—11.3 cm.

32703-50, collected 1979–80. One continuous band of bark stitched twice across the overlapping ends with cordage #3 tied off at the ends with knot "A." One string end finished off with knot "A." D—51.2 cm W—10.3 cm.

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OBITUARY FOR LEROY KERSHAW HENRY, 1905–1983

FREDERICK H. UTECH
Associate Curator in Charge, Section of Botany

LeRoy Kershaw Henry was born on 24 January 1905 in Pittsburgh, Pennslyvania, to Robert Watson Henry and Margaret Freeman Henry. He attended Zelienople High School, 1920–1924. On 8 December 1933, he married Elinor May Schatz and they raised four children—Carol (b. 18 August 1939), Earl (b. 5 June 1941), Clyde (b. 2 May 1944), and John (b. 5 June 1948).

Henry's long association with Carnegie Museum of Natural History began when he was an undergraduate, and he spent his entire career with the Museum and the Section of Botany. All of his collegiate education was at the University of Pittsburgh. He received his B.S. in 1928 majoring in botany and minoring in zoology, his M.S. in 1930, and Ph.D. in 1932. During the summers between 1928 and 1932 at a Boy Scout camp on Long Island, New York, he acted as a nature study instructor. His masters thesis and doctoral dissertation were entitled "Systematic and Ecological Studies of the Wading River Region, Long Island, New York" and "Mycorrhizae of Trees and Shrubs," respectively. His dissertation appeared in *Botanical Gazette* (1933) in an abbreviated form and was an early and significant contribution on the mycorrhizal association with woody species. He followed in the path at the Museum of his friend and mentor, Professor Otto Emery Jennings (Henry 1964, 1965). Henry moved up the ranks under Dr. Jennings from Museum Assistant (1928–29, 1932–37) to Assistant Curator in

Submitted 21 May 1985.

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Dr. LeRoy Kershaw Henry (1905–1983) working in the Carnegie Museum herbarium during the mid-1950s.

1937, to Associate Curator in 1946, and in 1947 he was promoted to Curator of the Herbarium. He requested an early retirement in 1973 due to a lingering case of Parkinson's disease and died on 19 November, 1983.

In his capacity as Curator of Botany, Henry spent much of his time identifying all groups of plants, native or exotic, including his own collections from all over the United States and Canada as well as those left in the herbarium by earlier collectors and those brought in daily by the public. Henry's interest in the vascular plants of western Pennsylvania led to several, co-authored county checklists: Allegheny County in 1951 with a 1964 update, Butler County in 1971, and Bedford County in 1978, as well as several regional monographs: Violaceae in 1953, Ranunculaceae in 1958, and Orchidaceae in 1955 and 1975. His interest in the ferns and their allies of the tri-state area lead to active collecting and photographing with hopes of producing a companion volume to *The Wildflowers of Western Pennslyvania and the Upper Ohio Basin* by Jennings and Avinoff. Henry served several times as Treasurer of the American Fern Society.

With the establishment and development in 1956 of the Museum's field station, Powdermill Nature Reserve, Henry was very active between 1957 and 1971 in producing educational and research reports on the various plants of the Reserve. For about ten years he and his wife, Elinor, and often their children as well, spent weekends almost monthly during the growing season searching and photographing the flora. He experimented with trial plantings of various legumes on spoil banks and learned that vegetative survival was not enough, unpalatability to deer was also required. Popular botany was further promoted by numerous articles which appeared in *Carnegie Magazine,* many illustrated by Elinor. Gardening and photography were among his favorite pastimes and they complemented well his field and herbarium work. Associated with the Botanical Society of Western Pennslyvania for nearly 53 years, he held the offices of Treasurer, Secretary, Vice-President, and President.

Henry's interest in native orchids caused him and his collecting companion, Werner E. Buker, to explore boggy areas throughout western Pennsylvania which were known to the Botanical Society, or reported to them. Henry's familiarity with such areas was most helpful to the Western Pennsylvania Conservancy in identifying small natural areas meriting preservation, such as Wattsburg Bog in Erie County.

Throughout his career, Henry concentrated on the taxonomy and ecology of the higher fungi of the tri-state area. He collected extensively in western Pennsylvania and identified thousands of specimens. Numerous popular and scholarly publications between 1933 and 1967 documented these studies. Voucher specimens were deposited in the herbarium of Carnegie Museum. In 1981, the fungus herbarium of Carnegie Museum comprising some 41,000 specimens, most collected regionally between 1900 and 1970, was exchanged to the New York Botanical Garden (Thiers, Desjardin, and Methven, *Brittonia,* 35:367–373, 1983) where it has been incorporated into their larger, international collection.

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